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AVIAN ENERGETICS

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FOREWORD¹

Nearly a decade ago, when the Nuttall Ornithological Club began to make plans for the observance of its Centennial, it was agreed that the occasion should be marked by an event which would be of genuine significance to ornithology. The centenary might have been observed, quite appropriately, for example, by reviewing the spectacular development of ornithology as a science, which has roughly coincided with the Club's 100-year history. This would have brought into focus the events of the past century, a needed and interesting enterprise, but the Nuttall Club felt it could better serve ornithology by fostering future advances; an historical approach was, therefore, abandoned.

After much consideration it was decided that the most suitable way to commemorate the past century and to enter a new century would be to organize a symposium on some topic that would be of paramount importance in 1973. But what would be important in 1973? To predict trends in a science nearly ten years in the future is risky. For guidance we solicited the opinions of many prominent ornithologists throughout the world. As one would expect, the prophecies were nearly as diverse as the prophets, but a thread ran through their responses which suggested that in the early seventies environmental physiology would be the discipline exhibiting the greatest activity and making the most significant advances in ornithology. To those prophets of the sixties, the Nuttall Club is grateful.

With the general topic of the symposium selected, we again canvassed our colleagues, this time for suggestions as to the person best qualified to organize the proposed meeting. On this occasion there was much less diversity of opinion, and the finger clearly pointed to William R. Dawson of the University of Michigan.

We met with Dr. Dawson and told him of our intention to make the symposium the major event in our centennial observance, as well as our mandate that this was to be a significant contribution to ornithology. He agreed with our aspirations and was appointed chairman of the symposium. To Dr. Dawson fell the responsibility for selecting a specific topic in the field of environmental physiology and for inviting the participation of the distinguished speakers and panel of discussants who are assembled here.

To permit this symposium to develop in depth, breadth, and coordination, and so that research would be oriented toward presentation at this meeting, the four principal participants were invited

¹ Remarks by the President of the Nuttall Ornithological Club, Raymond A. Paynter, Jr., at the opening of the Symposium on Avian Energetics, held on 10 October 1973 at Provincetown, Massachusetts, in observance of the Club's Centennial, and in conjunction with the 91st Stated Meeting of the American Ornithologists' Union.

FOREWORD

several years ago. They prepared manuscripts that were circulated among themselves and Dr. Dawson, and later were sent to the panel of discussants. These manuscripts have allowed me a preview of what will be covered today. It is evident that the Nuttall Club's wish to promote a significant contribution toward the advancement of ornithology will be amply met by this Symposium on Avian Energetics.

To you, Dr. Dawson, and to your eminent colleagues, the Nuttall Ornithological Club asks me to express our sentiments of both honor and pride in having your participation in the observance of our Centennial.

INTRODUCTION

WILLIAM R. DAWSON

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This is like Christmas in having the opportunity to arrange something that I'm interested in, to assemble some people for whom I have a great deal of respect and to let them go. I want to be as unobtrusive as possible, but I should like to suggest to you a general philosophical basis for this symposium. We are not implying here that this is the wave of the future and that everyone should drop all other aspects of avian biology. What we are suggesting is that over the centennial span of the Nuttall Club ornithology has moved progressively beyond some sets of concerns that primarily deal with just inventorying the North American avifauna, working out its systematics, and so on. These are still important. But now we have additional concerns. We have many analytical problems, for example, those relating to behavioral ecology. Additionally, a number of studies in evolution have found that birds constitute highly desirable model species for investigation. As a result of many of the things that involve such diverse topics as niche-breadth, species interaction, migration, all of which you heard about yesterday, or will hear about tomorrow in the AOU's Contributed Papers sessions, there are a variety of topics that have come to center, I think, upon one basic concern—and that is *energy*. You have here in this symposium a series of expositions on this concern, and you have added to it consideration of the factor of time. I think that with the careful arrangements that have been made in the dining room, you have become pre-occupied with your own time and energy, and are in a very receptive mood for what I hope will be a formidable contribution to avian biology.

I should like to take this opportunity before starting to introduce the discussants. I'll not identify the face with the name at this time because at the end of the contributions the discussants will take the series of chairs over here. You can recognize them because they'll be sharpening their knives as they come to the stage. But these three gentlemen whom I arranged to have serve as discussants constitute in themselves a very important reason for our being able to present this symposium. Their interests, in many cases their pioneering efforts, have led us really to have a field of avian environmental physiology.

Introducing them alphabetically, first of all, is Dr. George A. Bartholomew, from the University of California at Los Angeles. I, of course, am very impressed with this man. Surviving an early setback of

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having me as a graduate student, he has gone on to make very significant contributions to the field of avian physiology and to a variety of other things. He has a rather interesting contact with the Nuttall Ornithological Club in that, when he was a graduate student at Harvard, he was studying House Sparrows. He was procuring them from the ivy on buildings. He fell, suffered a severe concussion, and was subsequently treated by a then-young resident named Norman P. Hill, who is intimately concerned with the Nuttall Club. Now, in making this connection, it is very important that you understand that having a severe blow to the head is not a condition for being a discussant!

The next person that I would like to introduce is a man that has been very nice to me over the years and he is a real pioneer. I feel that he has the qualities of the type for which I should like to be recognized, should anyone ever refer to me as a pioneer, namely, that he continued to maintain a very active program in research on avian biology that has exerted a significant influence on the field of avian energetics. This is Dr. S. Charles Kendeigh of the University of Illinois.

Finally, I should like to point out to you that we have our ties with the general ecological community, through the Director of the Institute of Ecology at the University of Georgia, Dr. Eugene P. Odum. His credentials too, are impressive. He has been a significant force—and continues to be a significant force—in ecology generally and in avian biology particularly. This has in many instances manifested itself through a concern with avian energetics.

We have as our discussants then, Bartholomew and Kendeigh, who have been honored by the AOU with receipt of the Brewster Award in past years for their work. We also have Dr. Odum who, for the general work in the area of ecology and his direction-giving capabilities, has been elected to the National Academy of Sciences. I say all of this for two reasons. One is to tell you how proud I am to have them on the stage with me, and the other is to keep the speakers in line.

These speakers also comprise a very distinguished group. They are, in order of appearance, Dr. James R. King of Washington State University; Dr. William A. Calder of the University of Arizona; Dr. Robert E. Ricklefs of the University of Pennsylvania; and Dr. Vance A. Tucker of Duke University.

Dr. King has been given the extremely challenging task of analyzing the seasonal allocation of energy resources by birds, and he's done extremely well at it. He combines an excellent knowledge of avian biology with a rigorous approach to the physiology of birds. He is making substantial contributions to ornithology not only through his original research, but also through his efforts as coeditor, with Dr. Donald S. Farner, of the multivolume treatise *Avian Biology*.

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Dr. William A. Calder has been asked to discuss the energetics of birds in relation to body size. He brings to this topic experience in analyzing the size dependence of respiratory and circulatory variables in birds and, most recently, in investigating the energetics of hummingbirds nesting in montane situations. His work with hummingbirds in the Rocky Mountains is providing some fascinating insights concerning the physiological ecology of these diminutive animals.

Dr. Robert E. Ricklefs has published a number of widely cited papers on growth and reproductive patterns in birds, and he has been asked to deal with the energetic aspects of these processes in ecological perspective. He has drawn not only on his own work, but on a huge literature to produce a major synthesis. I am confident that his contribution to this symposium will constitute a major advance toward full analysis of the energy relations of crucial aspects of the biology of birds.

Major contributions to the analysis of the energetics of avian flight have come from the work of Dr. Vance A. Tucker, who will be our final speaker. This work reflects the incisiveness and technical ingenuity of its author. It has, along with developments occurring abroad, provided a basis for some generalizations concerning the flight process that I believe you will find intriguing, particularly as they relate to the energy requirements of migratory movements of birds.

SEASONAL ALLOCATION OF TIME AND ENERGY RESOURCES IN BIRDS

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INTRODUCTION

The essential continuity between an animal and its environment is revealed most obviously in energy exchanges and transformations. The maintenance of biological organization at all levels requires a basal and continuous flow of energy, supplemented intermittently in response to the demands of productive processes and variation in the physical and biotic surroundings. The energy flow can be partitioned conceptually into the maintenance of *physiological output* (heat, internal work, synthesis of compounds and tissues) and *behavioral output* (external neuromuscular work above the level expended by an isolated individual at rest). In another context, it can be partitioned into the requirements of *self-maintenance* and of *reproduction*. These dichotomies recur repeatedly in the literature (Root, 1967; Schoener, 1971; Verbeek, 1972) and in the following account, and provide useful perspectives even though the distinctions are often blurred or arbitrary.

TIME AND ENERGY RESOURCES IN BIRDS

The amount of food that an animal must procure per unit of body weight and time to maintain the minimal physiological and behavioral outputs consistent with self-maintenance and reproduction depends on an intricate interplay of many abiotic and biotic factors that include not only such obvious variables as micrometeorological agents, body size, the intensity of productive processes (growth, molt, gametogenesis), and the capacities for physiological acclimatization and temporary hypothermia, but also on the nature of competition and predation (e.g., Emlen, 1966), the nature of the social hierarchy and mating system (e.g., Orians, 1961, 1969), the grain of the environment with respect to food and shelter (e.g., Emlen, 1966, 1968), and so on. These less obvious factors affect an animal's food requirement by modulating the efficiency (gain per unit expenditure) of food-finding and feeding, and (or) they affect intake relative to requirement by modulating the time that an animal can devote to feeding instead of other functions indispensable to self-maintenance (e.g., aggressive encounters, avoiding predators, preening) and reproduction (e.g., courtship, territorial defense, nest building, incubation). The major factors affecting avian energy budgets, and some of their more obvious interactions, are depicted in Figure 1.

Energy and time are basically separate resources even though inter-related in complex ways (Orians, 1961). Energy intake (requiring the use of time) for the maintenance of essential functions and the allocation of time to these same functions cannot simultaneously be maximized (Wolf and Hainsworth, 1971). It follows as a reasonable hypothesis (Rosen, 1967) that natural selection has led to attributes that tend to optimize the allocation of time and energy required for self-maintenance and reproduction. It is thus not possible to understand fully the adaptive significance of energy budgets apart from time budgets, and we must deal ultimately with *time and energy* budgets, even though attention is focused in the present account on energy relationships. The resulting optimal patterns of allocation are adaptive "strategies" in the sense they tend to maximize fitness (Emlen, 1968; Schoener, 1971). Time and energy budgets are the only common denominator for analyzing the interacting effects of the diverse life history elements mentioned above, and this approach therefore offers a promising perspective for recognizing, eventually, comprehensive hypotheses about the evolution of adaptive strategies. A logical time unit for the examination of such strategies is one reproductive cycle, or one year in most avian species.

The ideal culmination of this essay would be a quantitative analysis of the seasonal variation of energy budgets for several representative types of annual cycles. This objective is not attainable at present except for one or two species on a very tenuous empirical basis. The future development of the subject will be served best by a summary of the fragmentary information that reflects the present "state of the art," by a review of the factors affecting time and energy expenditure, and

TIME AND ENERGY RESOURCES IN BIRDS

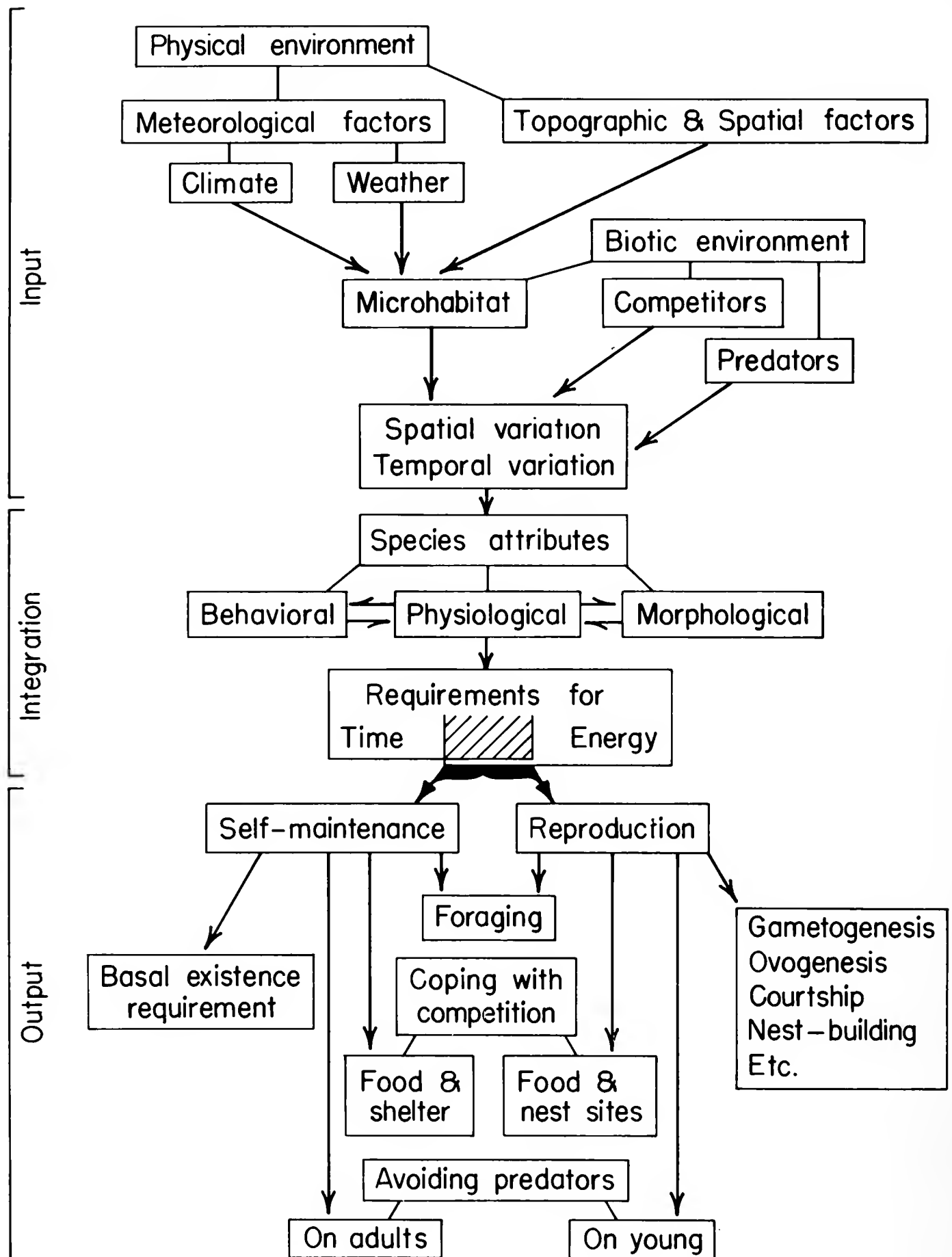


FIG. 1. Major variables and some of their interactions affecting energy requirements and seasonal variation thereof in free-living birds. Thin lines connecting boxes indicate subcategories; thicker arrows indicate interactions. Productive processes in self-maintenance (growth, molt) have been omitted to minimize clutter, but can be included in the "basal existence requirement."

by some guidelines for future investigations. These are the main intentions of the following account. It should be noted in passing that the phrase "energy budget" and its variants are used in at least three ways in the contemporary literature. First, the equations summarizing

TIME AND ENERGY RESOURCES IN BIRDS

energy exchange by physical routes are commonly called "energy budgets" or "heat budgets" both in organisms (e.g., Porter and Gates, 1969) and in inanimate objects (e.g., Lowry, 1969). Secondly, the trophic dynamics of ecosystems as well as component individuals may be described in terms of "energy budgets" (e.g., Petruszewicz and Macfadyen, 1970). Finally, the phrase "energy budget" is used to describe the partitioning of energy expenditure by individual animals in terms of basal maintenance, locomotor activity, and productive processes (e.g., McNab, 1963; Verbeek, 1964; Kendeigh, 1973). Used in this way the term is not always exact, since the income side of the "budget" is frequently disregarded; but the usage is so firmly embedded in the literature that it is unlikely to be uprooted at this stage. "Energy budget" is usually used in this third sense in the following account.

DIVERSITY OF ANNUAL CYCLES

Some appreciation of the complexity of time and energy budgeting in the annual cycle can be obtained from a survey of some of the ways that various species of birds allocate time and energy to major energy-demanding functions during the year. The annual cycle of a species includes all of the physiological, behavioral, and morphological adjustments that characterize its life in one year. Major energy-demanding functions are molt, reproduction, and migration, whose patterns and arrangement in time can be taken as simple indexes of interspecific variability in optimizing the annual allocation of time and energy. A generalized annual cycle in a migratory species consists of the sequence: winter residency/prenuptial molt (if any)/migration/reproduction/postnuptial molt/migration/winter residency. The simplest case of optimization of the major energy-demanding events is their complete or nearly complete separation in time, as is typical of many migrant species that breed at high latitudes. Departures (overlaps, seasonal offsets, deletions) from the strict separation of events may often be attributed to the pressures of time or shortages of energy. Some examples are cited in the sections that follow. Additional interspecific or intergroup variability may originate in differences in the mating systems or social systems, and the influence of these attributes must therefore be taken into account in any comprehensive analysis.

MIGRATION

The avian patterns of geographic translocation vary from (1) virtual nonmovement through (2) post-breeding dispersal of young, (3) local or altitudinal movements of whole populations, (4) nomadic or irruptive movements of whole populations or age groups, (5) latitudinal movements of parts of a species population ("partial migration"), to (6) the typical pattern of regular alternation of populations between fixed breeding and wintering grounds. The most plausible ecological interpretation of migration is that it is an adaptation that assures an ade-

quate food supply for self-maintenance or reproduction, or both (Lack, 1954). Migration may aid this objective in part by reducing the competition for limited food resources (MacArthur, 1959; Cox, 1968; Blondel, 1969) although this has overtones of group selection that may not be widely acceptable. These viewpoints gain support from the correlations that have been established between food supplies and the extent or timing of movement in partial migrants (e.g., Evans, 1966; Lack, 1968; Eriksson, 1970b) or nomadic or irruptive species (e.g., Newton, 1970; Eriksson, 1970a, 1971).

Dolnik (1971a) suggests on the basis of some indirect estimates that it would cost Chaffinches (*Fringilla coelebs*) about as much calorically to overwinter in Finland as it costs them to migrate to their more southern wintering grounds. In this case there is no caloric saving on an annual basis, but only a change in the site at which energy is obtained, presumably with greater efficiency. For the case of typical migration it is perhaps useful to think of species or even of populations of a given species as coevolving with respect to migratory or sedentary habits. Populations that have evolved a migratory habit have thus reduced breeding season competition for space and energy not only for themselves but also for sympatric winter populations that do not migrate, or that have evolved different patterns of migration. The White-crowned Sparrows (*Zonotrichia leucophrys*) of North America are a well-known example. Two or more subspecies may occur together in winter flocks mainly in the southwestern United States (Cortopassi and Mewaldt, 1965). The form *Z. l. nuttalli* is sedentary, breeding along the coast of California. *Z. l. pugetensis* migrates a short distance northward, breeding mainly along the coasts of Oregon, Washington, and southern British Columbia. *Z. l. oriantha* is also a short-distance and (or) altitudinal migrant, breeding in the alpine zone of the Sierra Nevada and southern Cascades, various isolated ranges of the Great Basin, and the Rocky Mountains into southern Canada. Finally, *Z. l. gambelii* is a long-distance migrant breeding mainly in Alaska and northwestern Canada. By coevolving distinct migratory properties that segregate them in the summer these four closely related forms thus avert conspecific competition during the critical periods of reproduction and molt. Many similar examples could be cited.

An essentially trivial corollary of the theory of natural selection is that migration will evolve if survival and reproduction are greater in migratory than in sedentary individuals, and conversely. Various patterns of migration can be rationalized by means of a mathematical model (Cohen, 1967) that optimizes survival and reproduction in alternative environments; but a more satisfactory rationale for migration will proceed at least one step further, to an identification of the constraints of food supply and of time and energy budgets that constitute the ultimate explanation for differences in survival and reproductive rate.

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MOLT

The patterns and timing of avian molt have an almost bewildering diversity that illustrates particularly well the evolutionary plasticity of the annual cycle. It is only recently that a significant modern synopsis of this diversity has been developed (Stresemann and Stresemann, 1966), emphasizing that we have only scratched the surface in our understanding of the adaptive significance of molt patterns in the world's avifauna as a whole. The generalized ancestral pattern was probably a relatively slow once-a-year replacement of the entire plumage, with a uniform ascendent sequence of molt in the remiges. This minimizes daily energy requirements while preserving the insulative and aerodynamic properties of the plumage (Stresemann and Stresemann, 1966). Permutations of this tempo and pattern no doubt represent compromises in the adaptation of birds to the concurrent constraints of time and energy, wear and tear of the plumage, maintenance of flying ability, and maintenance of the cryptic or communication functions of plumage color and pattern. The main variables upon which natural selection could act in optimizing adjustment to these often conflicting demands include the tempo of molt, the sequence of feather replacement within and among tracts, and the placement of molt, or molts, in the annual cycle. A few examples will illustrate how these modes of adjustment interact and in many cases reflect the pressures of time and energy supplies.

The duration of molt tends to be longest in birds living in environments in which seasonal change is least, as in resident tropical and subtropical species and many species of seabirds (Stresemann and Stresemann, 1966), and in migrant species that molt in tropical or subtropical wintering grounds. Molt may be essentially continual in tropical colies (Moreau, Wilk, and Rowan, 1948) and in some terns and other seabirds may be interrupted only during the breeding period (Ashmole, 1968). In contrast, particularly among migrants, there is a progressive shortening of the annual molt toward higher latitudes, at least in the Holarctic region, correlated with the greater seasonality of the environment and the short time between the end of breeding period and the onset of migration. Under the pressure of time, the annual molt may overlap the nesting period in a few species, and overlap contranuptial migration in others (examples will be cited subsequently). In extreme cases in the far north, passerine species that elsewhere display a gradual molt may shed the remiges almost simultaneously, and be rendered nearly flightless (Haukioja, 1971a; Salomonson, 1972).

The pattern or sequence of molt within and among tracts likewise shows extensive differences among species. Habitual simultaneous molt of the flight feathers, represented mainly in aquatic or marsh-dwelling species in eleven avian orders (Stresemann and Stresemann, 1966;

TIME AND ENERGY RESOURCES IN BIRDS

Woolfenden, 1967), is an extreme departure from the presumed ancestral pattern of gradual molt. In at least the loons, grebes, and alcids it has been argued that simultaneous molt of the flight feathers is an adaptation primarily to the aerodynamically inefficient wing, in which loss of even a single remex in each wing, as in gradual molt, would be a noticeable handicap (Savile, 1957; Woolfenden, 1967). The period of flightlessness can therefore presumably be shortened by a simultaneous molt, the reduced wing surface is probably an advantage to birds that feed by diving (Storer, 1971), and the adaptive significance of simultaneous remigial molt thus reduces ultimately in these cases to considerations of time and energy. Even given the temporal advantage of a simultaneous molt, it can be argued (Woolfenden, 1967) that at least adults of some of the larger loons (*Gavia immer*, *G. adamsii*, and *G. arctica*) do not have time to complete their annual molt on their northernmost breeding grounds without danger of being caught, or having their food supplies obliterated, in freezing lakes. These species winter in maritime habitats and delay the annual molt until late winter, thus assuring a more reliable food supply during molt and a fresh plumage for the spring migration.

Another variant of the basic ascendant sequence of remigial molt is the stepwise molt (*Staffelmauser*) that is found in all terns (Sterninae), most pelecaniforms, and in representatives (mostly tropical) of several other taxa (Stresemann and Stresemann, 1966). Stepwise molt involves the simultaneous initiation of molt waves in two or more loci of the remigial series. Stepwise molt is typically slow, usually occupying the entire period between breeding cycles (the rapid molt of the Arctic Tern [*Sterna paradisea*] while on its antarctic wintering grounds is exceptional), and in some forms may continue through the breeding period. It is improbable that a single hypothesis can fully explain the functional significance of stepwise molt in such a diverse taxonomic setting. Ashmole (1968) suggests that the stepwise molt continuously repairs the wings and preserves their aerodynamic quality better than the typical ascendent molt—a matter that would be particularly important to birds such as terns that search for food while flying. Whatever the evolutionary forces leading to a stepwise molt, a prolonged molt of this type obviously also spreads the energy cost of feather growth over a long period of time and thereby minimizes its impact on the daily energy budget.

Flight feathers and body feathers are usually replaced concurrently once per year in the annual (complete, postnuptial, or prebasic) molt. A minority of avian species (Stresemann and Stresemann, 1966) engage in one or more additional partial (prenuptial, or prealternate) or supplemental (Palmer, 1972) molts per year, and still fewer undertake two complete molts per year. The functional significance of the partial molt in some species (e.g., anseriforms, some species of ploceine weavers) lies in replacing the cryptic eclipse plumage, acquired in the annual molt, by the nuptial plumage. In species in which the partial molt in

adults produces no obvious change of plumage pattern (e.g., the crowned sparrows, *Zonotrichia*) the functional significance of the partial molt is enigmatic (King, 1972a).

Even in species typically having only one feather generation per year, the replacements of flight feathers and body feathers are not necessarily concurrent. In some cases the most plausible selective pressure favoring separate molts of these plumage components is the maintenance of the communication functions of the body plumage. The delayed molt of the body plumage in the Violet-backed Starling (*Cinnyrincinclus leucogaster*) for instance, assures a maximum plumage iridescence in the male at the onset of courtship (Traylor, 1971). In other cases, the separate temporal phasing of body molt and flight feather molt may result from constraints of energy supply or allocation. Extensive data are lacking on the relative weights (and hence energy requirement for replacement) of flight feathers and body feathers, but the detailed analysis of the Bullfinch (*Pyrrhula pyrrhula*) by Newton (1966) represents at least the small passerines and shows that the dry weight of the body and head feathers and coverts is 72% of the total dry weight of the plumage. This proportion is about 78% in House Sparrows in new plumage (Barnett, 1970) and about 75% in the White-crowned Sparrow (J. D. Chilgren, pers. comm.). The weight ratio of flight feathers to other feathers (including coverts) is about 2:1 in Steller's Jay (*Cyanocitta stelleri*) (Pitelka, 1958). It is likely that this ratio will be weighted even more heavily toward body plumage in short-winged, well-insulated birds, such as ptarmigan. It is thus evident that birds can significantly alleviate the daily energy cost of molting by uncoupling the usual phasing in circumstances that allow this adaptation. A well-known example of this is the Slender-billed Shearwater (*Puffinus tenuirostris*) which breeds on islands off the southeastern coast of Australia and winters (in the boreal summer) in the northern Pacific Ocean as far as 70°N. The adults complete the head-body molt on the breeding grounds, but the flight feather molt occurs only after the northward transequatorial migration (Marshall and Serventy, 1956a, 1956b). A similar complete separation of body molt and flight feather molt is also reported for the migrants *Emberiza melanocephala* and *E. bruniceps* (Stresemann and Stresemann, 1969a) and for various other species, both migratory and nonmigratory (Stresemann and Stresemann, 1966, 1969b). A partial, rather than complete, temporal separation of flight feather molt from head-body molt occurs in many other species, a particularly well-documented example being in adult Red-backed Sandpipers (*Calidris alpina*) breeding at 71°N (Holmes, 1966). Flight feather molt begins during the egg-laying period and continues into the postnuptial phase of slow southward wandering. Body molt begins at about the time that the eggs hatch, and may extend through the migratory season; but remigial molt is completed before the onset of migration.

The main form of adaptability in molt is its placement in the annual

cycle. Various permutations have already been cited. These take the form of interruptions of molt and (or) overlaps with other events of the annual cycle. Different geographic populations of a species may complete the annual molt on the breeding grounds, while others defer the molt for the wintering grounds (e.g., Stresemann and Stresemann, 1968a, 1968b, 1971, 1972). Only a few species engage simultaneously in molt and migration (Holmes, 1966; Dolnik and Blyumental, 1967). If begun on the breeding grounds, the molt is commonly suspended during migration, and resumed on the wintering grounds at the point of suspension (e.g., Baird, 1967; Stresemann and Stresemann, 1968a, 1971; Pimm, 1970; Gavrilov, 1971; Harris, 1971; Niles, 1972). Molt may completely or substantially overlap the breeding period in some species (e.g., Johnston, 1961; Maher, 1962; Nelson, 1964; Payne, 1965, 1969, 1972; Holmes, 1966; Snow, 1966; Stresemann and Stresemann, 1969c; Haukioja, 1971b), but may be suspended during the breeding season in others (e.g., Dorward, 1962; Snow, 1966; King, 1972), or suspended during the cold season (Stresemann and Stresemann, 1969c; Niethammer, 1970).

Finally, there are differences of molt schedules between sex and age groups that may reflect the pressures of time and energy resources. The sex difference is particularly well known in certain tetraonids and anseriforms in which the males take no part in rearing the young and begin the molt as soon as the mating season is over, the females typically deferring molt until the young are essentially independent. Regardless of the selection pressures leading to this temporal separation, the temporal offset of molt between the sexes may reduce the competition for food during a critical time. A similar interpretation may be correct for the delay of molt in immature Rufous-collared Sparrows (*Zonotrichia capensis*) in northern Argentina. The birds-of-the-year, regardless of age, begin the postjuvenile molt together at about the same time that the adults begin the annual molt (King, 1972a). Thus, competition is avoided with adults that are rearing young, even though competition is increased during the molting period. This can be interpreted as an evolutionary exercise in optimization. In the less seasonal environments of subequatorial Colombia (Miller, 1965) and Panama (Kalma, 1970), in contrast, young Rufous-collared Sparrows begin the postjuvenile molt when 50-60 days of age, regardless of the stage of the annual cycle.

A basically different selection pressure may be operating in the gulls *Larus argentatus*, *L. fuscus*, and *L. marinus*, in which the immatures begin the annual molt while the adults are still breeding. Harris (1971) suggests that the adults cannot afford to have imperfect wings while engaged in the work of feeding young, but immatures are free of this pressure. Likewise, the adults may not be able to support the concurrent cost of molting and feeding young.

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REPRODUCTION, MATING SYSTEMS, AND SOCIAL ORGANIZATION

The sexual and social characteristics of a species affect in many ways its temporal organization with respect to environmental seasonality. The commitment of time and energy to reproduction probably varies greatly from species to species. The energy costs of reproduction have been analyzed by Robert Ricklefs elsewhere in this volume, and therefore need to be mentioned only briefly in the present context. Suffice it to say that the costs of reproduction include all those attributable to the development and maintenance of the pair bond, if any, plus all subsequent behavioral and physiological costs associated with rearing young to the stage of independence. Interspecific variability in these costs originates (1) in differences of social organization and mating system (see beyond), and hence in the costs of courtship and space defense; (2) in the complexity of nest construction, if any; (3) in egg size and clutch size; 4) in incubation pattern and requirements; (5) in the condition of the young at the time of hatching (altricial or precocial) and in their growth rate; and (6) in the number of broods and the length of the nesting season. Some of these variables affect both sexes, but others affect only one; and hence energy budgets for the sexes must be treated separately specially during the breeding season.

Time and energy budget associated with reproduction (as well as with other elements of the annual cycle, to a less obvious extent) are affected not only by the mainly physiological factors summarized above, but also by the mating system and social organization of a species. Indeed, perhaps it is nearer the mark to interpret mating systems and social systems as the ultimate results of selection pressures than tend to optimize time and energy expenditure in events tending to maximize survival and reproduction.

For purposes of the present account mating behavior will be treated, arbitrarily, as distinct from social behavior. The mode of courtship and the nature of the sexual bond are the key attributes of the *mating system*. The dispersion patterns of individuals, pairs, and flocks, and the extent of territorial defense, constitute the *social system*. The adaptive significance of avian mating systems and social systems, in the context of individual fitness, has been thoroughly reviewed by Crook (1965), Lack (1968), and Orians (1969), and only some highlights relating the patterns to time-energy budgets need be presented here. In an alternative viewpoint, which will not be amplified here, Wynne-Edwards (1962) interprets these systems in the context of group fitness and population homeostasis.

With respect first to the sexual bond, about 92 percent of all avian species are monogamous, with a slightly smaller proportion among nidifugous than among nidicolous species (83 vs. 93 percent; Lack, 1968). Monogamy occurs mainly in species in which both parents feed the young or, if the young are nidifugous, escort and protect them; and

it can be argued logically (Lack, 1968: 148) that reproduction is typically maximized by the investment of time and energy by both parents. The reasons for the maintenance of monogamy are unclear in the exceptional species in which only one parent attends the young, although some plausible interpretations based on limitations of time or energy supplies have been proposed (Lack, 1968: 150).

Nonmonogamous mating systems (polyandry, and promiscuity) are found mainly but not exclusively in species producing nidifugous young that can feed themselves soon after hatching. It can be surmised that the attendance of a second parent does not improve reproduction rate, but may even reduce it through attraction of predators or competition for food. Among nidicolous species the reasons for the evolution of nonmonogamous mating systems are not easy to discern, but can plausibly be linked in many cases to the distribution of food or nest sites. At the risk of oversimplification it can be said that polygyny, polyandry, and promiscuity among nidicolous species have evolved mainly in permissive or unusual ecological circumstances in which the parent attending the young can rear them alone or with only the part-time assistance of the other parent (or, more rarely, with sibling or communal helpers). For instance, polygyny among passerines is closely correlated with "two-dimensional" habitats (Verner and Willson, 1966) such as marshes, plains, or savannas, in which food is densely stratified but often patchy (Orians, 1969), or in which suitable nest sites are not evenly distributed (Zimmerman, 1966). Under such circumstances some males can presumably sequester better resources than others (Orians, 1972) and reproduction can be optimized if females consort in common with such males.

Polygyny is also found in savanna-dwelling species that forage widely for food but nest in trees, which are few in number and widely spaced (Crook, 1962, 1964). This system is probably subject to a time-energy economy akin to "refuging" (Hamilton, et al., 1967; Hamilton and Gilbert, 1969; Hamilton and Watt, 1970). Other cases of polygyny are found among hole-nesting species that do not excavate their own nests, and in which there is a shortage of nest holes (von Haartman, 1954; Curio, 1959), and among tropical frugivores that raise nidicolous young. Some of the latter may be promiscuous rather than polygynous (Lack, 1968; Orians, 1972). For the case of the polygynous fruit-eating icterids, Orians (1972) suggests that the typically small clutch size allows the females to raise their small broods unaided, thus fostering the development of polygyny under the guidance of unknown selection pressures. The small clutch size of this group may result from a presumably limited capacity for protein synthesis by a frugivore, or be an evolutionary correlate of the typically low nest predation (but see E. S. Morton [1973] on the levels of nest predation in frugivores in general).

The social systems of birds are conveniently classified, for ecological purposes, on the basis of dispersion patterns (Crook, 1965; Lack, 1968; Brown and Orians, 1970). In the nonbreeding season, individuals may

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be solitary or gregarious, with subclasses in each category; and in the breeding season the social system may be "overdispersed" (territorial or solitary breeding units), colonial, communal, or based on arena behavior (Crook, 1965). The variability of dispersion patterns may be interpreted as the result of evolutionary modulation of aggressive behavior. In turn, aggressive behavior is usually employed by individuals in the acquisition of resources that tend to maximize survival and reproduction (Brown, 1964). In relation to social systems in the breeding season, prominent resources include food supply, nest sites, and mates. Competition will exist when these resources are present in less than optimal quantity for the number of individuals depending on them, and some or all of the resources will have to be defended through aggressive behavior. The defensibility of resources depends not only on spatial and social factors, but also on the economics of time and energy (Brown, 1964). Obviously, defense is counterproductive if so much time and (or) energy is spent in guarding or obtaining resources that the viability or fecundity of a reproductive unit is impaired. In this case the resource is not economically defensible, and systems involving opportunistic or nonexclusive exploitation will evolve. Protection from predation is an additional strong selection pressure in the evolution of social systems (Crook, 1965; Lack, 1968; Brown and Orians, 1970). Many examples are given by Brown (1964), Crook (1965), and Lack (1968) of the ways in which the aforementioned selection pressures have interacted to produce colonialism, communalism, typical territorialism, foraging assemblages, and so on; and these examples need not be repeated here. It may be suggested in conclusion that the identification of selection pressures in these theories is persuasive and adequate for the immediate objectives. Thoroughly general theories of mating systems and social systems, as in the case of the strategies of the annual cycle as a whole, must be developed on the basis of models of optimal time and energy budgets that ultimately explain the basis of survival and reproduction. This is an objective that appears to be far in the future. The remainder of this essay is devoted to an inventory of technology and the present state of knowledge in this field.

FACTORS AFFECTING ENERGY BUDGET

In the foregoing section I have identified in general terms the "ultimate factors" (in the sense of Baker, 1938), or selection pressures, that have influenced contemporary strategies in the seasonal allocation of time and energy resources. In the following section I focus attention on the "proximate factors" that influence an individual's time and energy budgets on a day-by-day or a seasonal time scale. These include a multitude of interacting physical and biotic elements of the environment.

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PHYSICAL FACTORS

The physical environment of a terrestrial animal consists of (1) micrometeorological agents such as temperature, thermal radiation, wind, and humidity that affect the animal directly, (2) other agents such as rainfall, tides, daylength, and snow cover that affect the animal indirectly by influencing the availability of food, and (3) topographic factors such as slope and exposure that may either intensify or ameliorate the impact of other physical factors. Even though this last category is often important in the analysis of microhabitats it will not be considered further in the present account (for review, see Geiger, 1966).

Factors Directly Affecting Energy Exchange

Avian ecologists have been slow to appreciate the complexity of microhabitats and the effects of micrometeorological agents on birds in spite of abundant investigations of micrometeorology and of the partitioned calorimetry of man and domestic animals dating back forty years. Perhaps beguiled by the ease of measuring air temperature, avian ecologists and comparative physiologists have until recently almost ignored other and equally important meteorological agents in spite of periodic reminders in the ornithological or ecological literature (e.g., Cartwright and Harrold, 1925; Kendeigh, 1934; Moore, 1945; Kelly, Bond, and Heitman, 1945) that the real environments of real birds include factors other than temperature.

The trend away from this simplistic view that has developed particularly through the past decade has been crystallized in an important contribution by Porter and Gates (1969) in which the four main physical environmental variables affecting heat budgets are identified as air temperature, thermal radiation, wind, and humidity (the elements of the "climate space"). The three main organismic variables are metabolic rate, water loss, and body temperature. A realistic treatment of an animal in its natural environment can be no simpler than this seven-dimensional system except in cases in which one or more elements (e.g., body temperature in a homeotherm) are constant. Calder and King (1974) have summarized these concepts together with avian examples, and they do not need to be reiterated extensively here. Suffice it to say that a significant knowledge of how avian energy budgets are affected by the physical environment must include not only experimental quantification of the coupling between a bird and its environment with respect to air temperature, radiation, humidity, and wind velocity, but also a quantitative definition of the bird's actual microhabitat with respect to these variables. These subjects are still in a primitive stage of development, although some noteworthy progress is being made (e.g., among many others, Johnson, 1957; Morrison, 1966; Schmidt-Nielsen, et al., 1965; Pruitt, 1947; Getz, 1971; Lowe and Hinds, 1971; Wathen, Mitchell, and Porter, 1971; Morgan and Old, 1972; Calder, 1973). Even a casual examination of Geiger's

(1966) summary of micrometeorological variables makes it plain that reliance on standard weather station data, so often used in the past in ecological accounts, may be grossly misleading in defining animal microhabitats and "climate space." Finally, at the risk of appearing to flail a straw man, it should be reiterated that the equations defining the caloric coupling of animals to radiation, wind velocity, and humidity require the use of air temperature data, directly, only in heat transfer by convection. In all other interactions air temperature is irrelevant or not directly relevant. It is time that this fact became more widely understood among ornithologists, and that measurements of thermal radiation, wind velocity, and humidity became routine in the analysis of avian microhabitats.

Factors Indirectly Affecting Individuals Through Food Availability

Various physical environmental agents that have no direct impact on minute-to-minute heat exchange may nevertheless strongly affect an animal's energy budget by modulating the availability of food. A few examples will illustrate the point. The insect food of aerial foragers (swifts, swallows, flycatchers, and so on) is particularly susceptible to low temperature, rain, and strong winds. Shelter-seeking, dormancy, aberrant feeding behavior, and mass starvation are reported for such species during periods of bad weather (Koskimies, 1950; Lack, 1956; Robins, 1971). In littoral feeders, food availability may be affected by substrate temperature (Goss-Custard, 1969), and waders may be forced to use unusual or alternative sources of food during high tides in periods of cold weather or short daylengths (Goss-Custard, 1969; Heppleston, 1971). Snow cover and ice cover may also affect avian foods in obvious ways. King and Wales (1964) correlated the daily feeding routine and local movements of rosy finches (*Leucosticte* spp.) with the depth of snow cover. Even in species of birds that cache food during winter and display an uncanny ability for locating the caches under snow as deep as 45 cm (Salfeld, 1969), the availability of the food must become sharply curtailed by weather producing an ice glaze over the snow surface (McGowan, 1969). Small birds such as redpolls (*Acanthis* spp.) that depend in part on feeding in subnival burrows (Cade, 1953) are probably also affected by ice glazes. Ice cover over water bodies likewise obliterates or restricts the food supplies of diving birds (e.g. Bianchi and Karpovich, 1969; Ainley and Le Resch, 1973). Finally, daylength itself is a physical variable that may affect the availability of food or the pattern of feeding. It is hypothesized that the long summer day and the greater time available for gathering food for young at high latitudes may be a selective pressure favoring the evolution of migration to such regions. Conversely, in at least some circumstances the short winter day coupled with cold weather may enforce feeding at night (e.g., Goss-Custard, 1969), although nighttime feeding, especially in anseriforms, is by no means restricted to periods of climatic stress (e.g., Swanson and Sargent, 1972).

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BIOLOGICAL FACTORS

The array of abiotic environmental factors described above interacts in diverse and subtle ways with an equally complex array of biotic variables in affecting avian energy budgets. The biotic factors can be logically subdivided into the attributes of the animal's phenotype and the biotic attributes of its environment, including the social environment.

Attributes of the Phenotype

Energy income and expenditure are influenced by physiological, behavioral, and morphological characteristics or modes of adjustment. The options in these categories are extensive and only some of the more important, or at least more obvious, of them will be mentioned.

Physiological Attributes.—Several modes of physiological adjustment may aid in ameliorating the influence of seasonal change in environmental conditions. Among these, thermoregulatory acclimatization is perhaps the best known (for review, see Chaffee and Roberts, 1971; Calder and King, 1974). Acclimatization, in contrast to minute-to-minute thermoregulatory responses, occurs over a span of days and leads to steady-state adjustments that tend to alleviate thermoregulatory stress. The physiological components of acclimatization to cold may vary among species, but in general include an improvement of tissue insulation, plumage insulation, and of the maximum sustainable metabolic rate. The net result is reduced energy expenditure in thermoregulation and improved survival time upon exposure to extreme cold. The avian patterns of acclimatization to heat are less well known than those to cold, but include at least an improved survival upon exposure to heat stress. The meager comparative data available at present tend to suggest that the powers of thermoregulatory acclimatization are well-developed in nonmigratory species of birds but are slight or negligible in migratory species (for summary, see Calder and King, 1974). This suggests that migratory forms have evaded selection pressures leading to the evolution of sensitive powers of acclimatization. A simple index of the powers of acclimatization (probably including also differences in genetic adaptation) in several avian species is shown in Table 1.

Allied with thermoregulatory acclimatization is hypothermia, which is a regulated decrease of body temperature reported for a few species of birds in conditions that threaten death from cold either from depletion of energy reserves or from an inability to balance heat loss by heat production. Hypothermia reduces the gradient for heat loss and, through the van't Hoff effect, the rate of heat production. Birds in a state of profound hypothermia are often described as "dormant," "torpid," or even "hibernating." Physiological details and examples are summarized by Dawson and Hudson (1970) and Calder and King (1974). Fragmentary observations scattered in the ornithological literature suggest that at least a mild hypothermia may occur in many

TABLE 1
Weight Loss in Selected Species Kept Overnight in Cages Without Food¹

Species	Mean annual body wt, g	Condition during winter		Condition during summer molt	
		Evening fat reserve, g	Nocturnal wt loss g/hr-m ² g/hr	Evening fat reserve, g	Nocturnal wt loss, g/hr
WINTER LATITUDE ca. 45°N <i>Carpodacus erythrinus</i>	24.4	0.8	22.1 0.17	0.5	0.25
<i>Emberiza hortulana</i>	24.4	0.7	17.8 0.15	0.2	0.26
WINTER LATITUDE ca. 55-60°N <i>Fringilla coelebs</i>	23.4	1.0	11.0 0.09	0.3	0.22
<i>F. montifringilla</i>	25.3	1.1	10.4 0.09	0.4	0.22
WINTER LATITUDE ca. 62-66°N <i>Carduelis spinus</i>	14.8	2.5	9.9 0.06	0.7	0.13
<i>Acanthis flammea</i>	18.0	5.0	7.2 0.05	---	---

¹ Captive birds retained and studied at the Biological Station at Rybatschi (ca. 55°N). Selected data from Dolnik, 1967.

species of birds (some of the better documented cases are summarized by Dawson and Hudson, 1970), but the trait appears to have evolved to the most conspicuous extent among very small-bodied birds (hummingbirds) and among groups habitually dependent on aerial feeding (swifts, goatsuckers, at least some species of swallows). Obviously, hypothermia, even though perhaps increasing the risks of predation, reduces the energy cost of existence and thus prolongs survival in the face of intolerable cold or inadequate energy supplies.

In addition to the purely thermoregulatory adjustments just mentioned, many species of birds store augmented supplies of energy in their bodies during periods of cold stress or enforced food shortage. This takes the forms of increased lipid reserves and (or) storage of food in the crop. The latter requires concurrent morphological adaptation, but is nevertheless conveniently considered in a physiological context.

The spectacular storage of fat that occurs in migratory birds as a supply of fuel for long flights (King and Farner, 1964; King, 1972b) and in some species of seabirds in conjunction with enforced starvation during incubation or molt (for review see Lack 1966; Ashmole 1971) are especially well-known examples of adaptation to special functions. Less conspicuous forms of energy storage also occur that are indispensable to day-by-day survival. In general, small birds in cold climates show an inverse correlation between air temperature and the magnitude of lipid reserves. Presumably this reflects an adaptation that improves overnight survival in the season of cold weather and long nights (King and Farner, 1966). Crude estimates (King, 1972b) show that the winter lipid reserves can usually supply only enough energy for overnight requirements and for initiating foraging on the following morning under prevailing environmental conditions, whatever they are. The maximum winter lipid reserves are typically much less than the reserves found in the same species during the migration season, which suggests that selection has not fully exploited the physiological capacity for fat storage during the winter, even in species that appear to have ample food supplies for the synthesis of fat (Evans, 1969). The reasons for this are not clear but perhaps reside in optimization of cost-benefit ratios. The energy and (or) time costs of obtaining food above maintenance requirements and of synthesizing superabundant reserves from it may be more expensive in terms of survival than the accumulation of reserves that are just sufficient for one night's survival in average conditions. The case appears to be an interesting model of evolutionary optimization and merits further study.

Overnight storage of food in the crop augments and (or) substitutes for lipid storage in some species of birds (Calder and King, 1974). One of the better documented examples is in the Willow Ptarmigan (*Lagopus lagopus*) in central Alaska, which show no winter fattening, but instead rely on packing the crop with food before retiring to nocturnal roosts (Irving, West, and Peyton, 1967; West, 1968).

On an hour-by-hour time scale the storage of food (nectar) in the crop is important in the time-energy economy of hummingbirds. A 3-gram hummingbird can store enough nectar in the crop to supply fuel for about 1 hr in flight or for about 4.2 hr at rest at $T_a = 20^\circ\text{C}$, or for 1.4 hr at 10°C (Hainsworth and Wolf, 1972). The supplies can be greatly extended if a hummingbird fills its crop just before becoming hypothermic (Hainsworth and Wolf, 1970). This theme is more fully developed in the following chapter by William Calder.

Additional physiological attributes affecting energy budgets include the group-specific intensities and durations of productive processes such as gametogenesis, growth, and molt. Robert Ricklefs analyzes the physiological energy costs of reproduction elsewhere in this volume. The energy costs of molt are widely assumed to impose a serious trophic or caloric stress on birds. Although this is probably true in some species and circumstances, the validity of the assumption should be critically examined for each case.

Behavioral Attributes.—In addition to the effects of patterns of migration, mating systems, and social systems mentioned in relation to the diversity of annual cycles, the time-energy budgets of birds are strongly influenced, in ways almost completely unquantified at present, by a variety of additional behavioral attributes. Behavioral thermoregulation is an important and sometimes crucial supplement to physiological modes of thermoregulation, and takes the forms of sheltering from environmental stresses, sunbathing, postural adjustments, and so on. Extensive treatments of behavioral thermoregulation are available in Dawson and Hudson (1970) and Calder and King (1974), and a detailed repetition is pointless in the present account. Suffice it to say that the physiological capacities of birds in relation to survival and to time and energy expenditure are greatly augmented by behavioral plasticity that tends to minimize the costs of thermoregulation.

Another important category of behavioral adaptation in relation to time-energy budgets is food storage or hoarding. This is a habit that is apparently most strongly developed in the Corvidae (for review see Turček and Kelso, 1968), but which is also widely known among other species, including woodpeckers (Kilham, 1963; McRoberts, 1970; Bock, 1970), nuthatches (Sviridenko, 1968), various species of *Parus* (Haftorn, 1956; D. Hart, 1958), shrikes (Durango, 1951; S. M. Smith, 1972), various raptors (Mayaud, 1950), and probably others. Food storage by herbivorous birds occurs mainly during autumn and is important in overwinter survival. Haftorn (1956) estimated that up to 60% of the food used by *Parus cristatus* in midwinter was obtained from caches made during the previous autumn. The late winter breeding of nutcrackers (*Nucifraga* spp.) and perhaps other corvid species in snow covered regions is no doubt made possible by exploitation of large caches of food (Turček and Kelso, 1968; Balda and Bock, 1971) and by morphological adaptations for food transportation and storage (Bock, Balda, and Vander Wall, 1973).

Morphological Attributes.—Body size is the foremost of the morphological factors that interact with physiological and behavioral constraints and options in affecting a bird's time-energy economy. William Calder elsewhere in this volume develops in detail the relations between body size and metabolic requirements. Briefly stated, animals tend to become more tightly coupled to physical environmental factors as body size decreases, and the proportion of metabolic power required by thermoregulation in the cold, therefore, is greater in smaller than in larger animals. This is ultimately reflected in food requirements and in time-energy budgets. For instance, Gibb (1954) found an inverse correlation between body size and time spent feeding in five species of birds in midwinter. Goldcrests (*Regulus regulus*) weighing 5 g spend essentially 100% of the daylight period actively feeding, whereas Great Tits (*Parus major*) weighing 18 g spent only 75%, and other species of *Parus* were intermediate in both weight and feeding.

Small body size should not uniformly be regarded as a bioenergetic disadvantage, since it may allow small birds to exploit favorable microhabitats that are inaccessible to larger birds. Furthermore, hypothermia as an adaptation to thermal or trophic stress is ecologically feasible only in small- or medium-sized birds (Calder and King, 1974; and Calder, this volume).

Attributes of the Biotic Environment

Many phenotypic traits of the kinds just mentioned interact with extrinsic biotic variables in ways that are reflected in time and energy budgets. The major extrinsic biotic variables include (1) the spatial distribution of food, nest sites, and shelter (an aspect of environmental "grain"), (2) the intensity of competition, and (3) the intensity of predation. The time and energy required to find, defend, and exploit environmental resources obviously depends on their distribution in space and time and on the intensity of competition for the same resources. In turn, the time and energy that can be spent in resource exploitation and other essential functions depends on how much must be spent in defense against predators. Several examples of such interactions have already been mentioned, and others (together with general or theoretical treatments) are offered by MacArthur and Pianka (1966), Emlen (1966, 1968), Horn (1968), Hamilton and Watt (1970), Orians (1971), Schoener (1971), and MacArthur (1972), among others. Even though these themes cannot be expanded to a useful extent in the space available here, it should be borne in mind that a narrow autecological approach is inadequate in the analysis of time and energy budgets. An organism's biotic environment as well as its physical environment can have profound effects on the ways in which it allocates its time and energy resources.

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ESTIMATION OF ENERGY BUDGETS

An analysis of annual or seasonal variation of energy expenditure depends on the integration of daily budgets. As will become apparent, the analysis of daily budgets is in a very primitive stage of development, and an improved technology is only now beginning to evolve. We have only small amounts of data for a few species of birds. Daily energy expenditure has been estimated in a somewhat larger variety of mammalian species, and selected data will be mentioned in a comparative context.

METHODS

The eventual goal in estimating energy expenditure in free-living birds is to ascertain not only the daily and seasonal totals, but also (and more importantly) to learn how the total is apportioned among the requirements of thermoregulation, food-gathering, space defense, reproduction, molt, and so on. The attainment of these objectives is extremely difficult, and no single extant method of measurement will suffice. The relations between real birds and real microenvironments are so intricate that empirical methods alone are hopelessly inadequate, at this point in time, in approaching realistic conclusions from a rigorous basis. A rigorous basis must take into account all of the principal variables of the heat budget equations and of life history phenomena. Empirical data must therefore be manipulated and supplemented by various methods of thermal modeling (e.g., Birkebak, 1966; Porter and Gates, 1969) and (or) behavior modeling (e.g., Pearson, 1954; Wolf and Hainsworth, 1971; Stiles, 1971; Schartz and Zimmerman, 1971). The methods that have been used up to the present time include (1) extrapolations from laboratory measurements of oxygen consumption or metabolizable energy intake, (2) time-motion studies of free-living birds, quantified in caloric terms by extrapolations of laboratory data, and (3) estimates of energy consumption by a variety of indirect methods in free-living birds. These methods and selected examples will next be summarized briefly (see, also, Gessaman, 1973).

Extrapolations of Laboratory Data

Estimates of minimal, near-minimal, or average daily energy requirements have been obtained by measuring oxygen consumption or metabolizable energy uptake of birds and mammals confined to respiration chambers or small cages. Studies are commonly made through a range of stable air temperatures, which is usually the only environmental variable quantified. Extrapolations or interpolations from such measurements have been used to estimate annual or seasonal energy budgets (e.g., West, 1960; Górecki, 1971; Grodziński, 1971; Kendeigh, 1973), the energy costs of incubation (El Wailly, 1968), molt

(Blackmore, 1969; Lustick, 1970; West, 1968), egg production (West, 1968), rearing of nestlings (Brisbin, 1969; Diehl, 1971), and the ecological limits of species distribution (e.g., Seibert, 1949; Salt, 1952; Wallgren, 1954; Zimmerman, 1965).

Measurements of Oxygen Consumption.—Measurements of oxygen consumption obtained from birds resting without food at night (or during their normal sleeping period) in a thermoneutral environment (not requiring extra energy for thermoregulation) approximate the minimal or basal metabolic rate (BMR). Measurements made under these same conditions but at air temperatures outside the thermoneutral range are a linear or near-linear function of air temperature below the thermoneutral range. Measurements made during the day (or normal active period) in quiescent but awake birds without food are often called the fasting metabolic rate (FMR). Within the thermoneutral range FMR averages about 25% greater than BMR (Aschoff and Pohl, 1970), which can be attributed to the greater muscle tonus and psychic activity of birds that are awake.

BMR and FMR are short-term measurements taken over a period of minutes. Oxygen consumption through the span of a day has also been measured in active and feeding animals confined to small cages (e.g., Pearson, 1960; West and Hart, 1966), and may be quantified as the average daily metabolic rate (ADMR) in relation to air temperature (e.g., Górecki, 1971; Grodziński, 1971). The relations among these and other measures of oxygen consumption are elaborated by Gesaman (1973).

Measurements of Metabolizable Energy.—Metabolizable energy is the energy obtained from food after the gastrointestinal and urinary wastes are subtracted. The metabolizable energy is subsequently expended as the heat increment of feeding (= calorigenic effect, or specific dynamic effect), and the requirements of thermoregulation, muscular activity, and productive processes. Part or all of the heat increment of feeding may be utilized in thermoregulation in cold surroundings, but the data are equivocal and the subject is still controversial (Calder and King, 1974).

Metabolizable energy intake by birds confined to very small cages that minimize expenditure in locomotion has been called *existence energy* by Kendeigh (1949), who pioneered the use of such measurements in an ecological context. Existence energy is regarded as the least energy needed by the animal to survive under conditions equivalent to the cage environment. Determinations are customarily made through a wide range of stable air temperatures indoors, and at several photoperiods. Existence (metabolizable) energy has proved to be a linear or near-linear function of air temperature in a variety of avian species (Kendeigh, 1949; Seibert, 1949; Davis, 1955; West, 1960, Cox, 1961; Martin, 1965; Zimmerman, 1965; Olson, 1965; Brooks, 1968; Blackmore, 1969; R. B. Owen, 1970). The maximum amount of metabolizable energy consumed by the bird at the limit of its cold

tolerance is called the *potential energy* (Kendeigh, 1949), or *ultimate metabolic capacity* (Kendeigh, 1973), and it is assumed that this level of intake is set by the capacity of the gastrointestinal machinery and is attainable at any other air temperature. The difference between ultimate metabolic capacity and existence energy is termed *productive energy*, and is the amount theoretically available to a free-living bird, in an environment affording unlimited food, for functions above the level of the existence metabolism. It should be borne in mind that existence energy equals BMR plus the energy costs of thermoregulation (if any) and of locomotion in the metabolism cage. It is assumed tacitly in the extrapolations of existence energy and productive energy that the cost of locomotion is minimal and constant; but it is well known that the intensity of activity of caged birds is strongly influenced by air temperature in some species but not in others (cf., Eyster, 1954; Zimmerman, 1965; Brooks, 1968). The locomotor activity index of redpolls, for instance, approximately doubled between air temperatures of -20°C and 30°C in experiments by Brooks (1968). Such cage activity may be ecologically meaningless (for a contrary opinion, see Dolnik, 1974b), and greatly complicates the interpretation of models based on the concept of existence metabolism. In the example cited, for instance, the increasing locomotor activity of redpolls with increasing air temperature inevitably decreases the slope of the line relating metabolizable energy to air temperature, and thereby produces a progressively greater underestimate of productive energy as air temperature increases. This source of error becomes negligible only in species that show no strong temperature dependence of locomotor activity (e.g., Zimmerman, 1965), or if the caloric cost of locomotor activity in every case is only a small fraction of total existence metabolism, which seems unlikely. It can be shown, in fact, from equations presented by Kendeigh (1970) that the ratio of the rates of existence metabolism to basal metabolism in birds weighing 15-25 g averages about 1.30, meaning that the increment above BMR due to locomotor activity in the cage is equal to about 30% of BMR in the thermoneutral zone.

In addition to the problems already mentioned in the use of laboratory data in extrapolations to field conditions, it should be noted that measurements of oxygen consumption in respiration chambers or of metabolizable energy in constant-condition rooms or cabinets are made under fixed conditions of air temperature, wind speed, humidity, and thermal radiation field. Fully rigorous extrapolations to free-living birds can be made only for each of these nearly unique sets of conditions. This is impossible in view of the fact that only the experimental air temperature and, less commonly, humidity are usually known or specified. Extrapolations are typically made from responses to experimental air temperatures to responses to standard meteorological air temperatures, such as the monthly mean, although microenvironmental conditions are sometimes taken into account (e.g., Pearson, 1960; McNab, 1963; King and Wales, 1964; Grodziński, 1970; Górecki, 1971).

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These extrapolations can be exact *only to the extent that air temperature alone is a sufficient parameter subsuming the potential for heat transfer in all routes of exchange*. It remains to be shown that this simplification is adequate for ecological purposes. Finally, animals confined to respiration chambers or to ordinary metabolism cages are deprived of many options for behavioral thermoregulation, and thermoregulation must therefore cost them more than it does under natural conditions. For instance, the slope of the line relating metabolizable energy intake to air temperature was 0.0094 kcal/g-day-°C in birds flying free in a large aviary, but was 0.0153 in birds kept in small cages in the same aviary, or $1.6\times$ greater (Weiner, 1970).

Extrapolations from Time-Activity Studies and Laboratory Data

Time-activity studies consist of recording the amounts of time that a bird spends in various activities, such as flying, foraging, singing, preening, sitting quietly, and so on. Such methods have been used in fragmentary or incidental ways for many years (e.g., Gibb, 1954; Pearson, 1954; Felix, 1958), but were first formalized as time-and-energy budgets in an extensive context by Orians (1961). For conversion to an energy budget the time spent in each activity must be multiplied by the caloric equivalent of the activity. Caloric equivalents are estimated from laboratory data and are in some instances of essentially unknown reliability. Recent examples of the method include the investigations by Stiles (1971), Wolf and Hainsworth (1971), Schartz and Zimmerman (1971), Collias, et al. (1971), and Utter (1971). The investigations by Utter (1971) and Utter and LeFebvre (1973) are of special interest because they estimate daily energy expenditure by time-and-energy budgets in parallel with D_2O^{18} metabolism in free-living birds (see beyond; also Mullen and Chew, 1973). For Purple Martins (*Progne subis*) the parallel estimates differed by a mean of 5 to 8% of the lesser value when it was assumed that $RQ = 0.8$. For Mockingbirds (*Mimus polyglottos*) the equivalent error was 6.7% if questionable determinations of D_2O^{18} are omitted. This reasonably close agreement provides confidence that estimates based on time-activity studies can produce reliable conclusions. This observation will be expanded in a later section.

Estimates of Energy Consumption in Free-living Birds

The time-and-energy methods just described are based in part on laboratory data extrapolated to the activities of free-living birds. The procedures described in the following paragraphs depend almost completely on the data obtained directly from free-living birds, even though in some instances requiring laboratory calibration of input-output relations.

Estimates Based on Changes of Body Weight or Composition.—If the change of body weight is known over a span of time in which a

bird does not feed (e.g., overnight, or during a migratory flight) and if the caloric equivalent of the weight change is known, then it is possible to estimate energy consumption during the same span. For simplicity, the variants of this procedure will be called *material balance* methods. A crude version of this technique was suggested by Taber (1928), and more intricate methods were devised by Helms (1963, 1968) for estimating overnight energy requirements in free-living birds. The method is also frequently applied in estimating the energy requirements of migratory flights (for review, see McNeil, 1969, 1972; Farner, 1970).

Material balance methods have the important advantage of allowing an estimate of the energy consumption of birds in their natural environment, but also involve a number of debilitating problems. First, they are almost always statistical, i.e., weight loss is rarely known for captured and recaptured individuals, but must be estimated as the mean of sample populations. Second, the accuracy of the method depends on a reliable estimate of the caloric equivalent of weight change, since this function appears as a multiplier in the equation: energy consumption = (kcal/ Δ weight) (Δ weight). The caloric equivalent of weight change does not have a unique value, but depends on the substrates being oxidized and the rate of pulmocutaneous water loss, as can be shown by some basic and simple considerations.

In a bird or mammal in which fecal and urinary losses of water are negligible in relation to pulmocutaneous loss (which is essentially true in the postabsorptive state) the only way in which weight can change is through absorption of oxygen and loss of carbon dioxide and water:

$$\Delta \text{Body wt} = \Delta \text{O}_2 - \Delta \text{CO}_2 - \Delta \text{H}_2\text{O}$$

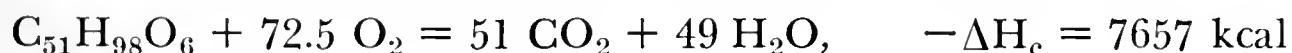
This equation can be rearranged to the form:

$$\Delta \text{Body wt} = \left[\frac{\Delta \text{O}_2}{\Delta \text{O}_2} - \frac{\Delta \text{CO}_2}{\Delta \text{O}_2} - \frac{\Delta \text{H}_2\text{O}}{\Delta \text{O}_2} \right] \Delta \text{O}_2$$

which is equivalent to:

$$\Delta \text{Body wt} = \left[1 - \text{RQ} - \frac{\Delta \text{H}_2\text{O}}{\Delta \text{O}_2} \right] \Delta \text{O}_2$$

The loss of body weight is therefore proportional to (1) oxygen consumption (metabolic rate), (2) the respiratory quotient (RQ), which in turn reflects the combustion mixture of fat, carbohydrate, and protein, and (3) the molar ratio of water loss to oxygen intake. In the simplest case in which a bird is oxidizing only fat (e.g., tripalmitin):



where $-\Delta H_c$ is the heat of combustion at constant pressure, the RQ is $51/72.5 = 0.704$, and the molar ratio of water production to oxygen

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consumption is $49/72.5 = 0.667$. Both values can be rounded to 0.7 for present purposes, and the equation given above reduced to:

$$\Delta \text{Body wt} = -0.4 \Delta \text{O}_2$$

In this preliminary step only the water produced in the oxidation of fat is assumed to be lost from the body, the water content of which is therefore stable. For a hypothetical case in which $\Delta \text{O}_2 = 224$ liters ($= 10$ moles, or 320 g) the weight loss is equal to $-0.4 \times 320 = -128$ g, and the energy consumption is equal to the oxygen consumed times its calorific equivalent at $\text{RQ} = 0.7$, or $224 \times 4.585 = 1050$ kcal. The caloric density of the weight loss is therefore $1050/128 = 8.2$ kcal/g. This is the theoretical upper limit of the caloric density of weight change for an unrealistic case. In all documented cases birds lose water faster through pulmocutaneous routes than they gain it by oxidation of metabolic substrates (Bartholomew and Cade, 1963). The ratio of water loss to oxygen uptake in small birds at rest in a thermo-neutral environment averages about 1.5 mg $\text{H}_2\text{O}/\text{ml O}_2$ (e.g., the Pyrrhuloxia [*Cardinalis sinuata*] and Common Cardinal [*Cardinalis cardinalis*]: Hinds and Calder, 1973), which is equal to a molar ratio of about 1.9. Inserting this realistic level of water loss into the equation for triglyceride oxidation yields a value of:

$$\Delta \text{Body wt} = -1.57 \Delta \text{O}_2$$

and leads, through manipulations like those already shown, to a caloric density of 2.09 kcal per gram change in body weight.

Similar estimates can be undertaken for other metabolic substrates, showing, for instance, that the caloric density of weight loss may be as low as 1.75 kcal/g in birds at rest metabolizing glucose exclusively. The salient point is that there is no standard or unique caloric equivalent of weight change, and each individual must be considered separately in terms of its nutritional status and state of water balance. The empirical determinations by Dolnik (1968) represent about the best that can be done with this method. Values tend to cluster between 5 and 7 kcal/g, but extend also to completely unrealistic levels (e.g., +11.5). It is evident that estimates of energy consumption based on this method can easily be subject to a large error.

Estimates Based on Crop Contents or Feeding Activity.—In avian species that show distinct diurnal cycles of feeding and food storage in the crop the gross daily energy intake can be estimated by methods outlined by Schmid (1965) for Mourning Doves (*Zenaida macroura*). This is a statistical method that requires large samples for reliable conclusions, and contains many sources of bias. Hintz and Dyer (1970), for instance, concluded from an analysis of stomach contents that the daily gross energy intake of Redwinged Blackbirds (*Agelaius phoeniceus*) was less than the estimated basal metabolic rate.

A similar method of estimating daily energy expenditure is based on the analysis of pellets cast by raptorial birds at habitual roosts, on

the assumption that all pellets are found. Graber (1962; see also Collins, 1963) determined the caloric equivalent of pellets cast by free-living owls, and thereby estimated daily energy consumption. The method is accurate if in fact all pellets are collected.

The quantification of daily food intake has also been attempted by continuous observation of the feeding activity of specialized feeders (e.g., Gibb, 1956; Murton and Westwood, 1963; Heppleston, 1971).

Estimates Based on Telemetered Heart Rate.—Attempts have been made from time to time to establish the reliability of heart rate as an index of metabolic rate (for reviews, see Morhardt and Morhardt, 1971; Johnson and Gessaman, 1973) and the method has recently been extended by R. B. Owen (1969a; Owen, Cochran, and Moore, 1969) to Blue-winged Teal (*Anas discors*) kept outdoors. The quantification of oxygen consumption by observation of heart rate is complicated by the fact that oxygen consumption is directly proportional not only to heart rate, but also to stroke volume and oxygen extraction from the blood. The most thorough exploration of the method is that of Morhardt and Morhardt (1971) for a variety of rodents. The data show in general that (1) metabolic rate as a function of heart rate is linear in some species and individuals but curvilinear in others, (2) that each animal must be calibrated individually in captivity before release, and (3) that even with thorough calibration the accuracy in predicting metabolic rate is $\pm 25\%$ to $\pm 150\%$. The authors conclude that the method in its present state is suitable for semiquantitative monitoring of changes of metabolic rate in free-living homeotherms, but yields only crude estimates of absolute metabolic rate.

Estimates Based on the Metabolism of Doubly Labelled Water.—The method of estimating CO_2 production (and thereby metabolic rate) by means of D_2O^{18} devised by Lifson, Gordon, and McClintock (1955) has recently been extended successfully to free-living animals. Briefly, the method depends on the fact that oxygen is lost from the body in both water and carbon dioxide, but hydrogen is lost only in water. The difference between the turnover rates is proportional to carbon dioxide production. The theoretical rationale is explained in detail by Lifson and McClintock (1966) and Mullen (1973). Fractional turnover rates can be quantified by injecting isotopic oxygen (as H_2O^{18}) and hydrogen (as D_2O), obtaining a blood sample after a period of isotopic equilibration, and a second blood sample after a timed interval. The isotopic content of water distilled from the blood samples must be determined by mass spectroscopy. Together with an estimate of the water content of the body, these data suffice to calculate the metabolic rate. The algebraic error of the method in validation trials in captive animals is 6-8% when compared with the results of the Haldane technique (LeFebvre, 1964; Lifson and McClintock, 1966; Mullen, 1970; Utter, 1970, 1971). The method has been applied successfully in free-living pigeons (LeFebvre, 1964), Purple Martins (Utter and LeFebvre, 1970, 1973), Mockingbirds (Utter, 1971), and several species of rodents

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(Mullen, 1970, 1971a, 1971b). It is undoubtedly the most accurate of the techniques applicable to free-living birds, but is expensive, moderately difficult technically, and requires recapture of the isotope-loaded animal. Attempts to estimate energy consumption by measuring the excretion of radioisotopes have not yet been successful (for review, see Sawby, 1973).

RESULTS AND ESTIMATES

This section first summarizes estimates of the rates of energy expenditure in various activities, continues with a résumé of time-activity studies of birds, and concludes with a consideration of daily and seasonal energy budgets.

Rates of Energy Expenditure in Various Activities

Basal Metabolic Rate.—Homeotherms that are not growing, molting, ovulating, or gestating function at the basal metabolic rate when in (1) muscular and psychic repose, (2) a thermoneutral environment, and (3) a postabsorptive state. Krogh (1916) coined the term "standard metabolic rate" (SMR) in applications to comparative physiology, and obviously regarded the term as synonymous with basal metabolic rate (BMR). The definition of SMR has subsequently been so mutilated and confused with the fasting metabolic rate (FMR), resting metabolic rate (RMR), and other late-blooming variants that I prefer to avoid the term altogether, reverting to the use of BMR in spite of my dissatisfaction with its clinical connotations (King and Farner, 1961). There is, at least as yet, no mistaking the definition of BMR.

Birds in their natural environments may not function for significant periods of time at the basal metabolic rate, and this measurement often has to be regarded as an abstraction in an ecological context. As a physiological standard, however, the BMR is an indispensable basis of comparison among the energy requirements of activities above the basal level because it is better defined functionally and statistically than any other component of the energy budget. Energy requirements above the basal level can be expressed as multiples of the BMR. The existence metabolism has occasionally been used for this purpose (see review by Gessaman, 1973), but the variable component of locomotor activity among species makes the existence metabolism a less reliable standard for comparative physiology. The BMR varies within a species with seasonal acclimatization (e.g., Veghte, 1964; Pohl, 1971; West, 1972a) and geographical origin (e.g., Hudson and Kimzey, 1966), and the mean rate for birds of the same size shows some taxonomic radiation (Zar, 1968), most notably between passerines and nonpasserines (Lasiewski and Dawson, 1967). These sources of variation must be taken into account in very exacting analyses, but are negligible (except the passerine-nonpasserine difference) in the present context.

In using the BMR for comparative purposes I have estimated avian

values from the equations of Aschoff and Pohl (1970; passerine and nonpasserines separately, in the rest phase of the daily cycle) and mammalian values from the equation of Kleiber (1961; see, also, J. S. Hart [1971] on rodents) except in cases in which the BMR is specified in particular investigations and departs widely from the allometric predictions. In such cases I have used the empirical data. When an estimate of BMR is used as the denominator of a ratio (see beyond), its error of course compounds the error included in the numerator. The data now available do not allow a statistical reduction of this problem except in a few trivial cases, and the ratios should be used only in identifying trends, levels, and ranges. Niggling examination of small differences is not only fruitless at this stage, but may be misleading.

The BMR is strongly weight-dependent, and can be expressed by the equation $\text{kcal/hr} = 4.78 W^{0.726}$ for passerine birds, and by the equation $\text{kcal/hr} = 3.60 W^{0.734}$ in nonpasserines, where W = body weight in kilograms (Aschoff and Pohl, 1970). (For conversion to SI units see Appendix.) The metabolic rate measured while a bird is awake during its normal activity period, but otherwise at muscular rest in a thermoneutral environment and in a postabsorptive state, is about $1.24 \times \text{BMR}$ in both passerines and nonpasserines (Aschoff and Pohl, 1970).

Increments Resulting from Locomotor Activity.—Flight, in spite of its intense energy requirement per unit time, is a relatively economical mode of transportation compared with walking or running. A 10-g bird flying 1 km is reported to use less than 1% of the amount of energy required by a mouse of the same weight running 1 km (Tucker, 1970). The maximal or near-maximal steady-state power output during exertion is an allometric function of body weight paralleling the function for the BMR (i.e., both are proportional to weight raised to about the 0.75 power). For a variety of organisms ranging from insects to horses, the maximal steady-state power output appears to be about $20 \times \text{BMR}$ (Hemmingsen, 1960). In mammals (rodents, lagomorphs, man) over a smaller range of weight the near-maximal steady-state power output averages about $6 \times \text{BMR}$ (Jansky, 1962).

For purposes of the present account it would be convenient to be able to express the power requirement of avian flight also as a uniform multiple of BMR, independent of body weight; but this subject is controversial at present and it is not clear that this simplification is legitimate. Birds may not fly habitually at the maximal steady-state power output, but rather at a lesser power expenditure (and speed) permitting attainment of maximal range. The "maximal range speed" may itself be a positive allometric function of body weight (Pennycuick, 1969). On theoretical grounds, Pennycuick (1969) concluded that the power requirement of avian flight is proportional to body weight raised to the 1.17 power. Subsequent amendments of theory (Tucker, 1973) for conditions in which the cost of transport is minimal yield the approximation: $\text{kcal/hr} = 72.8 W$, for birds of average wingspan,

and with body mass, W , in kg. This formulation predicts that power output in flight is a linear function of body mass, and by extension also predicts that the ratio of the power requirements of flight and of the BMR is $W^{1.0}/W^{0.72} = W^{0.28}$. Over a range from 0.01 to 10 kg this means that the ratio varies from about 6.2 to $43 \times$ BMR in nonpasserine birds and from about 3.8 to $26 \times$ BMR in passerines. These predictions do not conform well with empirical observations, especially by being incredibly high in larger birds.

Analysis of empirical estimates of power consumption by free-flying birds yields the equation: kcal/hr = $45.5 W^{0.73}$ (from Berger and Hart, 1972, with units converted; W = kg). A separate linear regression analysis of data for five species of birds and two species of bats summarized by Tucker (1970, 1973) yields the equation: kcal/hr = $55.7 W^{0.78}$, in which body mass, W , is in kg. This equation is not statistically distinguishable from the Berger-Hart equation.

It can be argued that the empirical scaling (exponent ca. 0.75) differs from the theoretical scaling (exponent ca. 1.17 or 1.0) because the empirical values were obtained from animals flying near the maximal steady-state power output rather than the power output for minimal cost of transport (maximum range speed). This argument cannot be usefully expanded at the present time, and the discrepancy between theoretical prediction and empirical observation must be resolved by further examination. While we should not be beguiled by analogies among empirical allometric relationships (BMR, maximal steady-state power output, power output in flight all proportional to $W^{0.75}$), we should not overlook, on the other hand, the fact that current theory extends at large body weights to levels of power output that are unknown among animals.

If the empirical scaling rather than the theoretical scaling of power requirement in flight in relation to body weight is accepted as correct, then the metabolic rate in flight has practically the same body weight dependence as the BMR, and can be expressed as a simple multiple of it. If the equations of Aschoff and Pohl (1970) for birds in the nocturnal or rest period of the daily cycle are used to estimate BMR, and the equation of Berger and Hart (1972) is used to estimate metabolic rate in flight, then the power requirement of flight is $9.3 \times$ BMR for passerines and $15.2 \times$ BMR for nonpasserines regardless of body weight. (There is no evidence in the scant data now available that power requirements of flight differ between passerines and nonpasserines as a function of body mass.) The average is about $12 \times$, a value that has been used by Utter (1971) and by Custer and Pitelka (1972) in quantifying time-energy budgets. Other investigators have used $5 \times$ or $6 \times$ multipliers for the same purpose (Orians, 1961; Schartz and Zimmerman, 1971). In many species that spend only a short part of the day in flight (see beyond) a two-fold error in estimating the metabolic rate in flight is probably negligible in the total energy budget. For species that depend extensively on soaring or glid-

ing flight the power requirement may be less than that for flapping flight and may thus fall below the $9-15 \times \text{BMR}$ of the allometric prediction. The power output in flight by Purple Martins, for instance, is $5-6 \times \text{BMR}$ (Utter and LeFebvre, 1970), and the estimates for other species of swallows and swifts are uniformly lower than those for species depending nearly exclusively on flapping flight (Farner, 1970). There may be, in addition, species-specific variations that are not revealed by the data currently available. A recent study of the Fish Crow (*Corvus ossifragus*) indicates that the cost of level flight at 18-20 km/hr is $8-9 \times \text{BMR}$ (Bernstein, Thomas, and Schmidt-Nielsen, 1972).

Relatively little is known about the power requirements of terrestrial or aquatic locomotion in birds. Power consumption during running is a linear function of velocity in birds ranging in body weight from 40 g to 22 kg (Taylor, Dmi'el, and Fedak, 1971; Fedak, Pinshow, and Schmidt-Nielsen, 1973). In this relationship smaller birds have a greater slope than larger birds, the weight dependence of power output following the equation: $\text{cm}^3 \text{O}_2/\text{g-km} = 2.3 W^{-0.2}$ (Fedak, Pinshow, and Schmidt-Nielsen, 1973), where W is in grams. In the case of a Greater Rhea (*Rhea americana*) running at 1 km/hr, the power output is about $3.5 \times$ the predicted BMR, and increases to about $14 \times$ at 10 km/hr (Taylor, Dmi'el, and Fedak, 1971). Presumably, hopping entails about the same relative energy expenditure, but this has not yet been quantified. Oxygen consumption in caged Chaffinches (*Fringilla coelebs*) is a linear function of the intensity of perch-hopping activity (Pohl, 1970), following the equation: $\text{kcal/day} = 10.84 + 0.00027 h$, where h = recorded hops per day. An increase from zero to 20,000 recorded hops per day thus entails an increase of about 50% in metabolic rate. The ecological significance of this is obscure at present.

The power requirements of surface swimming by birds have been investigated only in the Mallard (*Anas platyrhynchos*). Prange and Schmidt-Nielsen (1970) found that power output reached a minimum at intermediate velocities, as in the case of flight (Tucker, 1968; Pennycuik, 1969), at which point the cost of transport was minimal. The power consumption at this velocity was about twice that of the same ducks at rest in the tank, and about $3.2 \times$ the predicted BMR. At maximum swimming velocity the power consumption was about $5.7 \times \text{BMR}$. It was found that free-living Mallards tended to swim at the most economical velocity.

Increments Resulting from Maintenance and Reproductive Behaviors.—As already mentioned, the metabolic rate of fasting birds sitting quietly in the dark during their normal activity period is about $1.25 \times \text{BMR}$. This increment results from neuromuscular tonus and the psychic activity associated with wakefulness. Presumably, the energy expenditure of day-active birds in similar conditions but exposed to light would be still higher. In Chaffinches in such conditions the metabolic rate at air temperatures of 18-20°C is a linear function of the logarithm of light intensity, increasing about 30% on the

average between 1.0 lux and 100 lux (with much individual variation; Pohl, 1970). It appears from these data that the metabolic rates of quiescent birds during the day in the thermoneutral zone should fall in the range of $1.2-1.8 \times \text{BMR}$. This corresponds approximately with the ratios ($1.3-2.1 \times \text{BMR}$, averaging 1.7) predicted for five species of mammals by Taylor, Schmidt-Nielsen, and Raab (1970), and with the empirical ratio $1.68 \times \text{BMR}$ found by Wolf and Hainsworth (1971) in the hummingbird *Eulampis jugularis*. It can be calculated from the appropriate equations of Kendeigh (1970) and Aschoff and Pohl (1970) that the existence energy metabolism of passerines in the 15-50 g weight range averages $1.5 \times \text{BMR}$ at $T_a = 30^\circ\text{C}$, and that of nonpasserines averages $1.35 \times \text{BMR}$. These estimates of course involve the entire 24-hour cycle of metabolism, including the period of nocturnal rest, and the ratios therefore differ from those given above for awake but quiescent birds.

Although modern fast-response instruments allow direct measurement of functions that are included in time-energy budgets (such as singing, preening, foraging, and displays), the energy costs of these functions do not appear to have been quantified empirically except in a few cases. The oxygen consumption of Long-billed Marsh Wrens (*Telmatodytes palustris*) engaged in unspecified activity in a darkened metabolism chamber during the day, averaged $1.5\times$ that of wrens at rest in the same conditions (Kale, 1965: 66). The existence (metabolizable) energy consumption of White-throated Sparrows (*Zonotrichia albicollis*) forced to hop or flutter at about 0.14 km/hr in a revolving drum for 12 of 14 hours of darkness in an LD 10:14 photocycle was about $1.3\times$ that of controls that were sedentary at night (Kontogiannis, 1968). If it is assumed that the rate of existence metabolism is about $1.5 \times \text{BMR}$, then the difference between exercised and sedentary birds in this experiment is about $2 \times \text{BMR}$.

The observations by Deighton and Hutchinson (1940) and Hutchinson (1954) of the correlations between various activities and heat loss in domestic fowl in a low-lag direct calorimeter, although sometimes cited as examples of the energy cost of these activities (e.g., Whittow, 1965; Freeman, 1971), do not accurately quantify the costs of activity increments. The sharp peaks of heat loss associated with crowing, gaping, and changes of posture result in part from the sudden release of warm air entrapped in the plumage, and thus exaggerate the increments of heat production resulting from these activities.

Extensive empirical data on levels of energy expenditure in various activities appear to be available only for man and domestic animals (e.g., Passmore and Durnin, 1955; Brody, 1945). Some selected data for man are shown in Table 2. Because of the parallel allometric relationships between body weight and BMR and, tentatively, between body weight and the cost of locomotor activity, respectively (Brody, 1945; Aschoff and Pohl, 1970), it is reasonable to assume that the ratios shown in Table 2 are independent of body weight, since both men and

TABLE 2

Activity Levels in Man as Multiples of BMR¹

Activity	xBMR
Daytime dozing	1.2
Light sedentary work	1.3
Standing activities	1.7
Walking	5.8

¹Data from Passmore and Durnin, 1955.

birds are bipedal. These should be accepted only tentatively, however, pending empirical measurements. It is known that the horse, for instance, has the same metabolic rate in both standing and supine positions. This is unlike other domestic quadrupeds (Brody, 1945) and is assumed to result from skeletomuscular suspensory attributes unique to the horse. The possibility of a similar situation in birds should not be overlooked.

Avian ecologists have used BMR, resting metabolic rate (RMR), and existence energy as bases for estimates of activity increments, which makes comparison among sets of methods subject to substantial error. Utter (1971) estimated that the energy cost of nonflight activities was $2 \times \text{BMR}$ in free-living Purple Martins and Mockingbirds. Custer and Pitelka (1972) estimated for the Lapland Longspur (*Calcarius lapponicus*) that resting during the day cost $1.5 \times \text{BMR}$, and that feeding and incubating cost $3 \times$ and $1.65 \times \text{BMR}$, respectively. Schartz and Zimmerman (1970) assumed that the energy expenditure of the Dickcissel (*Spiza americana*) resting during the day was equal to the measured existence energy, which is roughly $1.5 \times \text{BMR}$. The cost of foraging was estimated as $1.7 \times$ existence energy, or roughly $2.6 \times \text{BMR}$. Orians (1961), in constructing time-energy budgets for Red-winged Blackbirds, based his estimates on the resting metabolic rate and used $1.1 \times \text{RMR}$ for singing and $2 \times \text{RMR}$ for displays. If it is assumed that $\text{RMR} = 1.7 \times \text{BMR}$, then the cost of singing is $1.9 \times \text{BMR}$, and of displays $3.4 \times \text{BMR}$. Such unsatisfactory conversions can be avoided in the future if estimates of activity increments are based uniformly on the BMR.

Increments Resulting from Productive Processes (Molt).—The energy required in the day-by-day repair of body tissue is allocated to productive processes but is included in the BMR. Productive processes above this level in birds comprise gonadogenesis, gametogenesis, ovogenesis, growth, molt, and the production of nutrient fluids such as crop milk and stomach oil. The energy costs of these processes are equal to the energy content of the new tissues or substances plus the cost of synthesizing them. The ratio of the energy content of the new animal product to the energy used above the maintenance level to form the product is the *partial efficiency* or *net efficiency* of synthesis (Kleiber, 1961). If the energy content of the product and the partial efficiency are known, then the total cost of production can be calculated. Robert Ricklefs discusses the costs and efficiency of reproduction and growth in another chapter in this volume, and attention will therefore be confined here to the energetics of molt.

The dry weight of the plumage is a weak allometric function of body weight (i.e., essentially a linear function of body weight), following the equation:

$$P = 0.09 W^{0.95}$$

where plumage weight (P) and body weight (W) are in grams (Turček, 1966). The plumage weight of a hypothetical 1-g bird is therefore 9% of total body weight, the proportion apparently decreasing to 8% at 100 g, 6.4% at 1 kg, 5.7% at 10 kg, and so on. The feathers of a 100-g bird, for instance, thus constitute about 27% of its total dry weight if the water content of the body (less feathers) is estimated as 68% (Turček, 1966). Contour feathers and coverts comprise about three-quarters of the total feather weight, and quills about one-quarter, in small passerines (e.g., Newton, 1966; Barnett, 1970), but there are no doubt substantial variations from the averages in both total feather weight and fractional weights among taxa (Turček, 1966).

The foregoing data supply some insights into the amount of feather material that must be synthesized during a complete replacement of the plumage, but do not tell the entire story. Each growing feather contains at its base a section of highly vascular pulp, which makes up as much as 22% of the total length (and up to 53% of the total weight) of the feather in the domestic fowl (Lillie, 1940). The pulps represent an extension of the blood-vascular system through the surface of the body that is unique among terrestrial animals. Coupled with the presumably defective plumage at least during the early part of the molt, this increased flow of blood to the surface must greatly augment heat loss and thereby increase the cost of thermoregulation (although heat loss may be minimized by a vascular countercurrent heat exchanger; see Figs. 18 and 19 in Lillie, 1940). The total caloric costs of molt therefore include the synthesis of the new feather material, the synthesis of the pulp vascular system and added blood volume that it requires, the extra cardiovascular work in supplying the pulp caps, and

the extra costs (if any) of thermoregulation resulting from the condition of the plumage.

It is apparent in birds that molt large parts of the plumage simultaneously, such as the flight feathers, that the replacement of the plumage is a severe nutritional stress in terms of energy requirements as well as amino acid requirements (for review, see Hanson, 1962). Birds that undergo a typical sequential molt have less intense burdens. In at least some cases in captives (Davis, 1955; West, 1968) the daily energy intake is no greater during molt than before or after it, owing perhaps to a compensatory reduction of other energy-demanding functions during feather replacement. However, there have been no detailed investigations of the energy budget of any avian species during molt, and our present knowledge of the energetics of this process is very limited. Investigations thus far have entailed measurement of oxygen consumption and existence metabolism during molt.

Oxygen consumption in a (single) Chaffinch under standard conditions at $T_a = 10^\circ\text{C}$ was consistently higher during molt than before or after it, reaching a peak of about 30% above the premolt level coinciding with the onset of remigial molt. The average oxygen consumption through the entire molt period was about 13% above the premolt level. Oxygen consumption was about the same before and after the molt period (Koch and deBont, 1944). Similar studies of molting Yellow Buntings (*Emberiza citrinella*) and Ortolan Buntings (*E. hortulana*) in the thermoneutral zone revealed increases of 14-26% above the BMR of nonmolting birds (Wallgren, 1954). Oxygen consumption in domestic fowl at room temperature has been shown to increase by about 15% during the molt, compared with premolt levels (Gerhartz, 1914). In other studies of domestic fowl at $T_a = 28^\circ\text{C}$ the increase was about 45% (Perek and Sulman, 1945), with a large range of variation.

Molting Brown-headed Cowbirds (*Molothrus ater*) compared with premolting controls through a range of air temperatures ($5\text{-}40^\circ\text{C}$), consumed oxygen at a rate about 13% above that of controls at $T_a = 35^\circ\text{C}$ in spite of identical whole-body conductance (Lustick, 1970). Below the thermoneutral range the conductance (= heat-transfer coefficient) of molting birds was slightly but consistently greater than that of controls, and oxygen consumption was about 24% greater than that of controls at all air temperatures. Surprisingly, the regression lines relating metabolic rate to air temperature were essentially parallel in molting and nonmolting birds. The regression line for molting birds should have a steeper slope if, in fact, whole-body conductance is greater in these birds than in those with intact plumage. Lustick (1970) proposes that the 13% increase of metabolic rate observed in the thermoneutral zone represents the cost of synthesizing feathers, and the additional 12% increase observed below this zone results from increased expenditure in thermoregulation.

Additional attempts have been made to quantify the caloric costs of

molt by measuring metabolizable (existence) energy income in birds confined to small cages at constant air temperatures. The energy expenditures in locomotor activity as well as in molt (and other productive processes) are variables in this situation. To estimate the increment of metabolizable energy associated with molt it must be assumed that the locomotor activity is the same in premolt, molt, and postmolt test periods and at the various experimental temperatures. This is usually unknown and always unlikely. Free-living birds are more secretive and less active during the postnuptial molt than at other times of the annual cycle (e.g., Newton, 1966; Haukioja, 1971b) and locomotor activity in caged small birds also diminishes during the molt period (e.g., Eyster, 1954; Weise, 1956). This probably explains why the metabolizable energy income was the same or less in molting House Sparrows (*Passer domesticus*) compared with nonmolting individuals kept in the same conditions (Davis, 1955). It is unlikely that molting involves no net caloric cost. The studies of oxygen consumption already mentioned clearly indicate otherwise. Blackmore (1969), also investigating the existence energy metabolism of House Sparrows, asserts that increased insulation provided by the growing feathers almost compensates for the cost of synthesis, so that the mean daily metabolizable energy intake during molt is increased by only 0.9% at $T_a = 3^\circ\text{C}$, by 3.9% at 22° , and by 8.6% at 32° . The increases of metabolizable energy intake at the peak of molt, compared with premolt controls, are estimated as 17% at 3°C , 21% at 22° , and 35% at 32° . Owing to a complex but unspecified program of statistical analysis it is difficult to trace these conclusions back to the original data. Moreover, there is no indication that variation in the energy costs of locomotion was constant or negligible. Investigations of the metabolizable energy intake of molting birds are of interest in showing that the *total* energy intake at the time of molt may be the same as in nonmolting birds (Davis, 1955) or increased slightly (e.g., West, 1960, 1968; Blackmore, 1969; Dolnik, 1971b), thus presumably reflecting a compensatory change in the partitioning of energy expenditure. The extent to which such data can be extrapolated to free-living birds is unknown, and the subject merits continued examination.

Daily Energy Expenditure in Free-living Birds and Mammals

Energy budgets and time budgets are intimately interlocked, and a significant understanding of many life history phenomena and adaptive strategies requires a joint analysis of both time and energy allocation. The extant empirical data are inadequate for a generalized treatment of this subject, and hypothetical models (e.g., Schoener, 1971) have to be developed largely without the assistance of empirical insights. As a contribution toward quantifying future models I have attempted in the following sections to summarize information on energy expenditure in free-living birds and to compare the results with similar data for rodents (there are but few suitable data for other taxa of mammals;

for review see Gessaman, 1973). This summary first includes a treatment of total daily energy expenditure, of necessity disregarding day-by-day or seasonal variations. A brief section then follows concerning what little is known of phasic or seasonal variations. When possible, parallel data for time expenditure are included.

Total Daily Energy Expenditure.—The minimal caloric flow required to support normal health and body weight in domestic animals in the usual conditions of husbandry when not gestating, lactating, laying eggs, molting, or growing is customarily called the maintenance metabolism. This includes the BMR, any extra costs of thermoregulation, the heat increment of feeding, and the cost of muscular activity in feeding and comfort movements. Maintenance metabolism is thus analogous to the “existence energy” (Kendeigh, 1949, 1972) of wild species of birds kept in small cages. The rates of both the maintenance metabolism (Brody, 1945) and existence energy metabolism (Kendeigh, 1970) in or near the thermoneutral zone tend to parallel the BMR as allometric functions of body weight (i.e., in data sets spanning an analytically significant range of body weights, the slope coefficients approximate 0.75). This suggests the hypothesis that the average daily metabolic rate of free-living homeotherms may be a similar allometric function of body weight, but it is not intuitively obvious whether this is true or false. The *modus vivendi* of most species of animals may not be faithfully reflected in the energy budgets of domesticated or captive individuals. The hypothesis can be examined through the summary of available estimates of total daily energy expenditure in free-living birds and rodents (Tables 3 and 4). The daily energy expenditure is abbreviated as DEE, following Utter (1971) and Utter and LeFebvre (1973). The estimates of the ratio DEE/BMR range between 1.7 and 6.1 for nontorpid individuals (see beyond), and fall mainly between 2 and 4. This relatively narrow range of ratios indeed suggests that DEE is an allometric function of body weight, paralleling the function for BMR. The data span nearly two log cycles, and thus allow a meaningful allometric analysis. (For a thorough treatment of this subject see the chapter by William Calder in this volume.) To explore this further, I have disregarded the heterogeneous conditions underlying the estimates of DEE and have combined all data in Table 3 in the calculation of the least-squares regression for birds:

$$\log \text{DEE} = \log 317.7 + 0.7052 \log W$$

where DEE is in kcal/day, W is body weight in kilograms, $S_{\log Y, \log X} = 0.1110$, $S_b = 0.186$, $r = 0.97$, and $n = 18$ (Fig. 2). The slope of the regression line, 0.705, does not differ significantly from the slope coefficients for the dependence of BMR on body weight computed by Aschoff and Pohl (1970). Because of the limited data for DEE it is not useful to compute separate equations for passerines and nonpasserines, analogous to those for BMR, but there is no suggestion in Figure 2

TABLE 3
Estimates of Total Daily Energy Expenditure (DEE) of Free-living Birds.

Species	Body wt g	Conditions	DEE		DEE Method ¹		Source
			kcal/day	kcal/g-day	BMR		
<i>Asio flammeus</i>	406	Illinois, winter	188	0.46	5.4	A	Graber, 1962
<i>Asio otus</i>	252	Illinois, winter	159	0.63	6.1	A	Graber, 1962
<i>Zenaidura macroura</i>	120	N. Dakota, autumn	49.7	0.33	2.7	B	Schmid, 1965
<i>Aegolius acadicus</i>	96	Illinois, winter	59.0	0.61	3.4	A	Graber, 1962
<i>Progne subis</i> , ♂♂	47.7	Minnesota, breeding	34.1	0.72	2.7	C	Utter and LeFebvre, 1970
<i>Progne subis</i> , ♀♀	50.2	Minnesota, breeding	43.9	0.87	2.9	C	Utter and LeFebvre, 1970
<i>Mimus polyglottos</i>	48.9	New Jersey, breeding	28.8	0.59	2.3	C	Utter, 1971
<i>Spiza americana</i> , ♂♂	35.0	Kansas, breeding	24.4	0.70	2.4	C	Schartz and Zimmerman, 1971
<i>Passer domesticus</i>	29.0	Illinois, January (max.)	28.0	0.96	3.2	E	Kendeigh, 1973
		Illinois, August (min.)	19.8	0.68	2.3	E	Kendeigh, 1973
<i>Calcarius lapponicus</i> , ♂♂	28.6	Alaska, breeding, early	40.0	1.48	4.6	D	Custer and Pitelka, 1973
<i>Calcarius lapponicus</i> , ♂♂		Alaska, breeding, late	25.0	0.93	2.8	D	Custer and Pitelka, 1973
<i>Calcarius lapponicus</i> , ♀♀	25.4	Alaska, egg laying	32.0	1.26	4.0	D	Custer and Pitelka, 1973
<i>Parus major</i>	18.0	England, winter	22.5	1.25	3.6	F	Gibb, 1957, 1960
<i>Anthus spinoletta</i>	12.0	England, winter	12.0	1.00	1.7	G	Gibb, 1956
<i>Calypte anna</i> , ♀♀	4.8	Central California, breeding, 21 January	6.7	1.39	3.0	D	Stiles, 1971
		Central California, breeding, 22 March	7.8	1.63	3.6	D	Stiles, 1971
		Central California, nonbreeding, September	7.0	1.46	3.2	D	Stiles, 1971

¹ A, pellet analysis; B, crop-contents; C, doubly labelled water; D, time-activity budget combined with laboratory data; E, extrapolations from laboratory data; F, extrapolations from food consumption of captives; G, observation of feeding rate and excretion rate.

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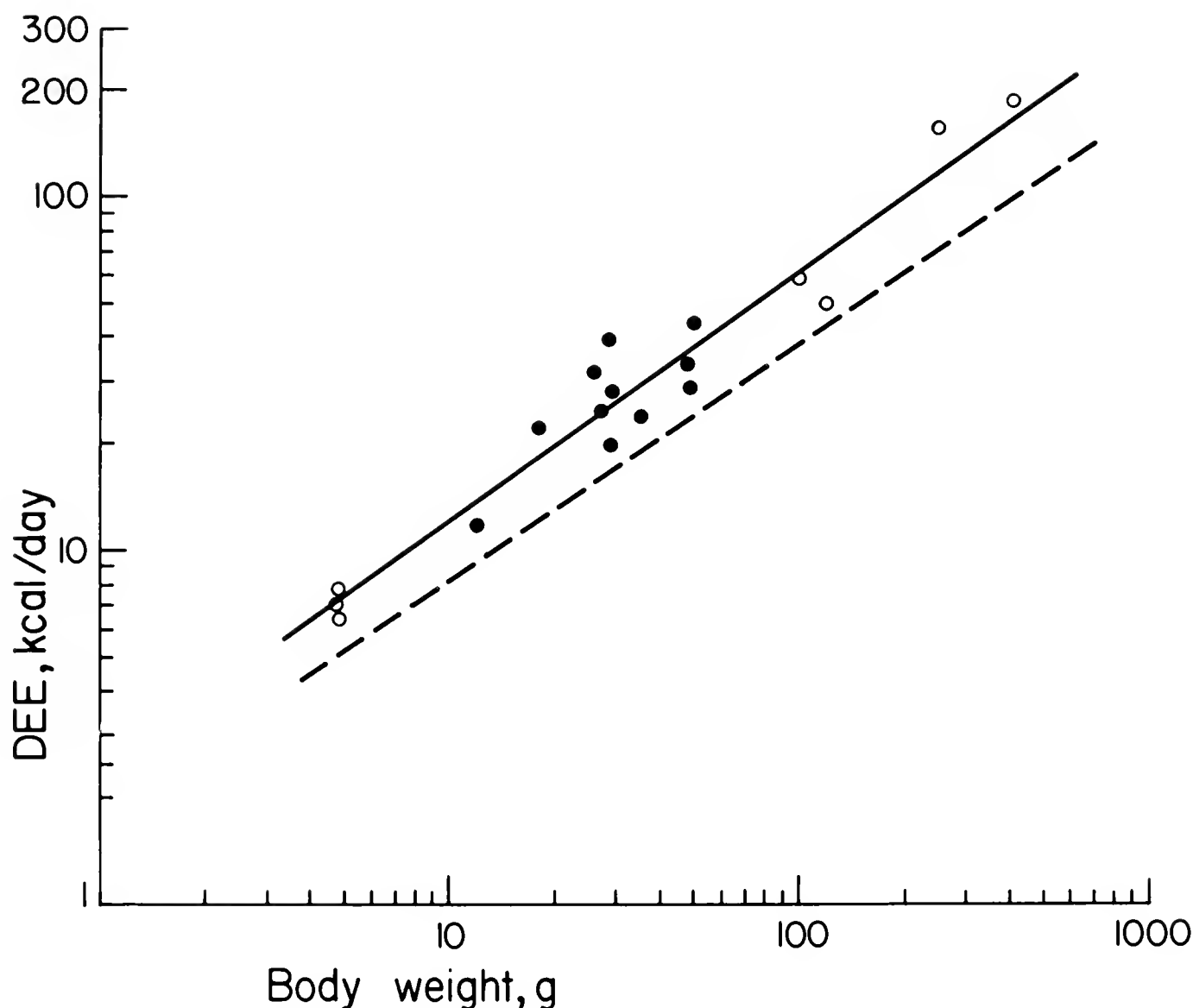


FIG. 2. Least-squares regression (solid line) of daily energy expenditure (DEE) on body weight in free-living birds (data from Table 3). Blackened circles denote passerine species, and unblackened circles denote nonpasserine species. The broken line depicts the regression for free-living rodents (Fig. 3).

that these data sets follow separate regressions. The DEE/BMR ratio in this sample of birds averages about 3.5 (calculated from the ratios in Table 3 rather than the ratio of allometric equations).

For rodents (Table 4), analogous computations yield the equation:

$$\log \text{DEE} = \log 179.8 + 0.6687 \log W$$

and $S_{\log Y, \log X} = 0.1040$, $S_b = 0.213$, $r = 0.95$, and $n = 19$ (Fig. 3). To match as well as possible the avian data, in which all but three of the estimates of DEE are from breeding or overwintering birds, maximal values of DEE for rodents were arbitrarily selected (the boldface numerals in Table 4). The slopes of the regression lines for birds and rodents do not differ significantly ($0.75 > P > 0.50$), but the elevation of the avian line above the abscissa is significantly greater than that of the rodent line ($P < 0.001$). The bird/rodent ratio of Y -intercepts at 1 kg is about $318/180 = 1.77$, thus supporting the common belief that free-living birds function at a relatively high metabolic intensity.

Assuming that the slope of the rodent line does not differ significantly from the slope (ca. 0.75) of the general mammalian equation

TABLE 4
Estimates of Total Daily Energy Expenditure (DEE) in Free-living Rodents.

Species	Body wt g	Conditions	DEE		Method ¹	Source
			kcal/day	kcal/g-day BMR		
<i>Spermophilus franklinii</i>	607	Nebraska, late winter-spring	124	0.22	2.8	E Haberman and Fleharty, 1971
<i>Tamiasciurus douglasii</i>	243	British Columbia, adult ♂, July	94	0.39	2.2	D C. C. Smith, 1968
<i>Tamiasciurus douglasii</i>	290	British Columbia, adult ♀ with 3 pups, July	175	0.60	3.6	D C. C. Smith, 1968
<i>Glis glis</i>	158	Poland, spring	45.1	0.29	2.6	E Gebczyński, et al., 1972
<i>Glis glis</i>	147	Poland, autumn	27.4	0.19	1.6	E Gebczyński, et al., 1972
<i>Dipodomys microps</i>	53.9	Nevada, October (min.)	2.9	0.053	0.4	C Mullen, 1971a
<i>Dipodomys microps</i>	62.9	Nevada, June (max.)	37.6	0.60	4.3	C Mullen, 1971a
<i>Dipodomys merriami</i>	31.7	Nevada, August (min.)	6.2	0.20	1.4	C Mullen, 1971a
<i>Dipodomys merriami</i>	39.5	Nevada, March (max.)	29.9	0.66	4.3	C Mullen, 1971a
<i>Dipodomys merriami</i>	37.7	S. California, June (min.)	9.4	0.25	1.5	E Chew and Chew, 1970
<i>Dipodomys merriami</i>	41.1	S. California, December (max.)	18.7	0.46	2.8	E Chew and Chew, 1970
<i>Peromyscus californicus</i>	49.6	Hypothetical, June	10.2	0.21	1.8	E McNab, 1963
<i>Peromyscus californicus</i>	49.6	Hypothetical, February	15.8	0.32	2.8	E McNab, 1963
<i>Peromyscus truei</i>	33.3	Hypothetical, June	10.2	0.32	1.8	E McNab, 1963
<i>Peromyscus truei</i>	33.3	Hypothetical, February	15.2	0.46	2.6	E McNab, 1963
<i>Microtus arvalis</i>	20.0	Poland, January	8.7	0.44	2.3	E Trojan and Wojciechowska, 1969
<i>Microtus arvalis</i>	20.0	Poland, July	9.2	0.46	2.5	E Trojan and Wojciechowska, 1969
<i>Microtus agrestis</i>	21.0	S. Sweden, autumn	11.0	0.52	3.1	E Hansson and Grodziński, 1970
<i>Microtus agrestis</i>	20.4	S. Sweden, winter	10.6	0.52	3.1	E Hansson and Grodziński, 1970
<i>Microtus agrestis</i>	23.8	S. Sweden, summer	12.3	0.52	3.1	E Hansson and Grodziński, 1970
<i>Apodemus agrarius</i>	22.5	Poland, winter	11.6	0.51	2.8	E Tertli, 1972
<i>Dryomys nitedula</i>	23.7	Poland, spring	15.3	0.66	3.6	E Gebczyński, et al., 1972
<i>Dryomys nitedula</i>	25.3	Poland, autumn	13.1	0.52	3.0	E Gebczyński, et al., 1972
<i>Muscardinus avellanarius</i>	20.2	Poland, spring	12.9	0.64	3.4	E Gebczyński, et al., 1972
<i>Muscardinus avellanarius</i>	19.0	Poland, autumn	7.96	0.42	2.2	E Gebczyński, et al., 1972
<i>Perognathus formosus</i>	18.6	Nevada, August	7.4	0.40	2.1	C Mullen, 1970

TABLE 4 (continued)
Estimates of Total Daily Energy Expenditure (DEE) in Free-living Rodents.

Species	Body wt g	Conditions	DEE		Method ¹	Source	
			kcal/day	kcal/g-day BMR			
<i>Perognathus formosus</i>	18.6	Nevada, October	14.3	0.77	4.0	C	Mullen, 1970
<i>Perognathus formosus</i>	18.6	Nevada, August	6.6	0.36	1.8	E	Mullen and Chew, 1973
<i>Perognathus formosus</i>	18.6	Nevada, October	11.3	0.61	3.2	E	Mullen and Chew, 1973
<i>Peromyscus maniculatus</i>	19.0	Hypothetical, June	8.4	0.44	1.9	E	McNab, 1963
<i>Peromyscus maniculatus</i>	19.0	Hypothetical, February	12.9	0.68	3.0	E	McNab, 1963
<i>Clethrionomys glareolus</i>	21.0	Poland, winter	10.2	0.49	1.8	E	Górecki, 1968
<i>Clethrionomys glareolus</i>	19.0	Poland, summer	10.6	0.56	2.1	E	Górecki, 1968
<i>Clethrionomys glareolus</i>	15.4	England, summer	22.3	1.5	4.1	E	Meese, 1971
<i>Peromyscus crinitus</i>	12.4	Nevada, November	7.9	0.64	3.5	C	Mullen, 1971b
<i>Peromyscus crinitus</i>	16.0	Nevada, February	16.9	1.05	5.7	C	Mullen, 1971b
<i>Reithrodontomys megalotis</i>	9.0	California, June	6.6	0.74	4.4	E	Pearson, 1960
<i>Reithrodontomys megalotis</i>	9.0	California, December	8.6	0.96	5.6	E	Pearson, 1960
<i>Micromys minutus</i>	8.7	Poland, annual	8.6	0.99	1.7	E	Górecki, 1971

¹ C, doubly labelled water; D, time-activity budget combined with laboratory data; E, extrapolations from laboratory data, usually combined with temperatures of microhabitat.

for BMR (Kleiber, 1961; J. S. Hart, 1971), the DEE/BMR ratio for the rodents, computed as the quotient of allometric equations, averages $180/70 = 2.6$, compared with about 3.5 in birds. Speculation regarding the bioenergetic significance of these levels and apparent differences would be premature. The data available for this introductory exploration are few and heterogeneous with respect to conditions of measurement. While I do not believe that additional data will alter the conclusion that DEE parallels BMR as a function of body weight, both this representation and the estimates of DEE/BMR ratios are subject to substantial numerical error and biased by a very limited taxonomic representation. The numerical estimates presented here must be continuously scrutinized and amended as more and better data on DEE become available. The averages and ranges of DEE/BMR ratios nevertheless aid, even at this stage, in an examination of the plausibility of individual DEE estimates. Ratios that deviate greatly from the predominant range may result from faulty measurements of DEE (or from group-specific peculiarities of BMR) or may reflect extraordinary conditions that merit special attention. Selected cases of these types are as follows.

Among birds (Table 3), the DEE of *Anthus spinoletta* was estimated by a difficult procedure involving field observation of the rates of defecation and of the intake of food of known caloric content. For a winter period when the mean temperature on the coast of Cornwall was 4.5°C the estimate of DEE appears to be too low, even though falling near the regression line. The DEE/BMR ratio falls considerably below that of animals undergoing minimal stress (Table 5).

At the other end of the scale, Graber (1962) estimated the metabolizable energy consumption of free-living owls by a method of pellet analysis. The accuracy of this method depends heavily on fulfilling the assumptions that each owl regurgitates one pellet per day, that all pellets were found at the roost, and that the number of owls per roost was known. Long-eared Owls (*Asio otus*) and Short-eared Owls (*Asio flammeus*) roosted gregariously, but Saw-whet Owls (*Aegolius acadicus*) were solitary (Graber, 1962). This may help to explain why the estimates for the first two species (more owls than known?) are outside the predominant range of DEE/BMR ratios in Table 3 and above the regression line in Figure 2, while the data for the Saw-whet Owl are within the range and on the line.

Other estimates that depart conspicuously from the predominant ranges in Table 2 are the DEE (40 kcal/day) and the DEE/BMR ratio (4.6) for male Lapland Longspurs early in the breeding season. The DEE was estimated from time-activity data (Custer and Pitelka, 1972), and coincides with the two-week period of courtship flights. Flying time (20% of total time) was quantified calorically as $12 \times \text{BMR}$, which may overestimate the power consumption of courtship flights that involve much gliding.

In rodents, the values of both DEE (Fig. 3) and the DEE/BMR ratios

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(Table 4) average lower than those of birds (even though maximal values of DEE were selected in the data for rodents), but the DEE of 2.9 kcal/day for *Dipodomys microps* is clearly aberrant (DEE/BMR = 0.4). These data were obtained in October from a single individual

TABLE 5

Daily Energy Requirements of Domestic Animals.¹

Species & conditions	Body wt. kg	Metabolizable energy (ME) kcal/day	<u>ME</u> BMR
Horse			
Maintenance	635	18,415	2.1
Medium work	635	27,305	3.1
Hard work	635	34,290	3.9
Dairy cattle			
Maintenance	545	14,715	1.9
Beef cattle			
Maintenance	500	16,500	2.2
Swine			
Pregnant	227	10,215	3.0
Lactating	205	16,400	4.3
Sheep			
Maintenance	59	3,540	2.4
Chicken			
Adult hen, laying	1.82	273	2.4

¹ Data from Albritton, 1954.

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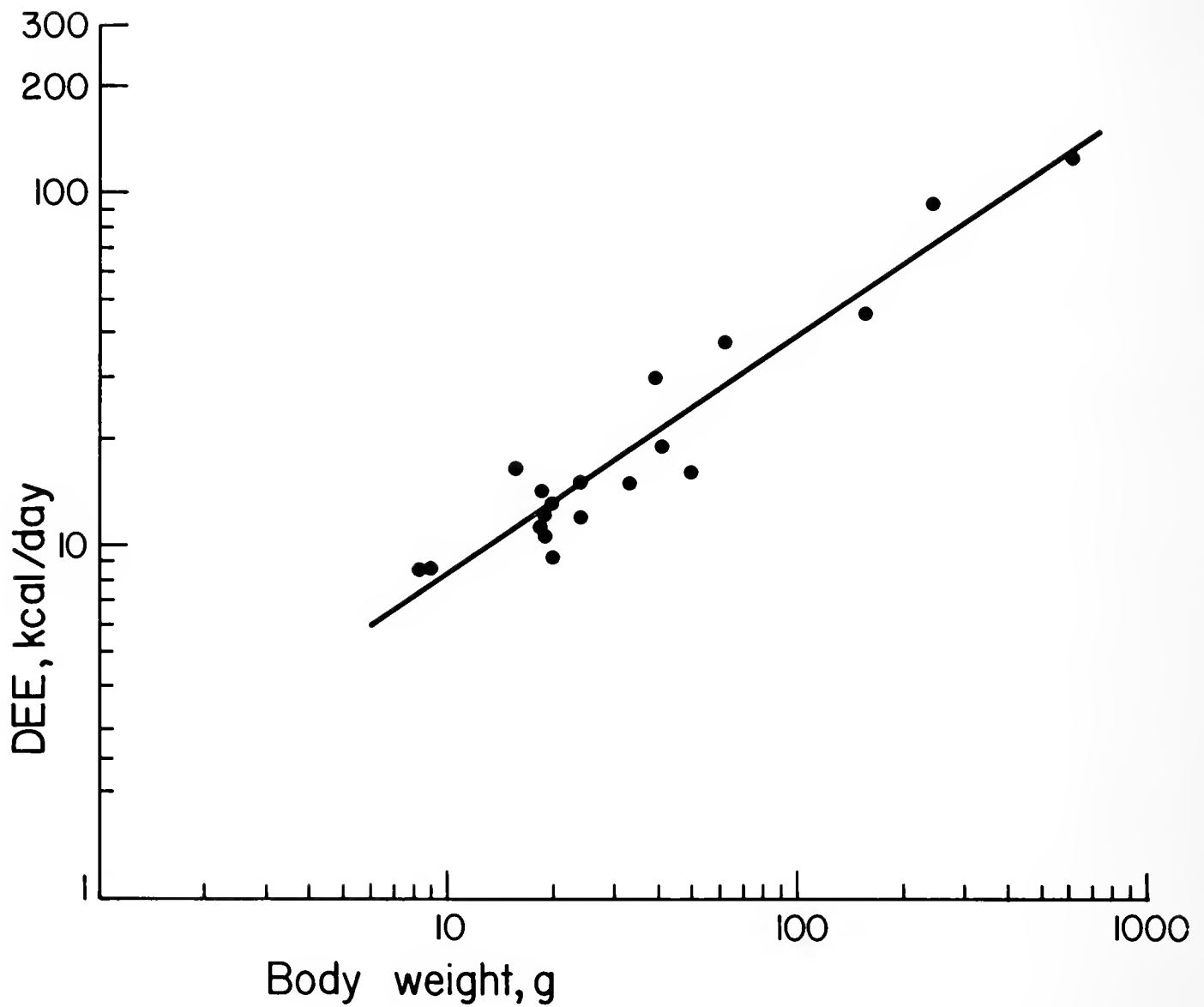


FIG. 3. Least-squares regression of daily energy expenditure (DEE) on body weight in free-living rodents (data designated by boldface numerals in Table 4).

in which DEE was measured by the D_2O^{18} method. Another individual measured in November showed values only slightly higher, and Mullen (1971a) argues that this results from diurnal hypothermia or torpor in cold weather. Data for *Dipodomys merriami* (Mullen, 1971a) show a complex dependence of DEE on air temperature that also suggests the occurrence of diurnal hypothermia, although the evidence is not fully persuasive. Aberrations traceable to hypothermia would be equally or more likely in *Perognathus* spp., but were not observed (Mullen, 1970).

The highest DEE/BMR ratio in Table 4 (and DEE substantially above the regression line in Figure 3) is 5.7, obtained by the D_2O^{18} method for a single individual in February. This ratio is approached only by that for *Reithrodontomys megalotis* in December (DEE/BMR = 5.6, but DEE near the regression line). The next highest ratios are 4.3-4.4. Although the unusually high DEE/BMR ratios for *Dipodomys* spp. may result from faulty measurements in two individuals, it would be unwise to dismiss them as such at this stage. Mullen (1973) shows that the D_2O^{18} method gives consistently reliable results in captive rodents, and the reasonably close conformity of independent estimates of DEE by D_2O^{18} metabolism and by indirect methods in free-living *Perognathus formosus* (Mullen and Chew, 1973) adds confidence in the

reliability of the D_2O^{18} method in the field. The unusually high DEE's in the cases cited may result from activities that elude indirect modes of estimation; the unusually high DEE/BMR ratios may result from this and (or) depressions of BMR attending hypothermia; and so on. The questions cannot be resolved at this stage, and further speculation is pointless.

The data just reviewed support the tentative conclusion that non-torpid free-living homeotherms tend to operate within the range of about 1.5 to 4 times BMR, with birds functioning at substantially higher relative levels, on the average, than rodents. Utter (1971) has expressed a similar opinion, and has proposed that three "priority levels" can be identified with respect to energy expenditure. Priority Level I is associated with individual maintenance, and Utter suggests that it ranges from 1.2 to 2.1 times BMR. Individuals at this level are hypothetically completely isolated from conspecifics, and have time budgets consisting mainly of foraging, resting, and body maintenance.

Priority Level II is associated with the maintenance of social structure and has a proposed energy cost of 1.6 to 2.6 times BMR. In addition to the activities of Priority Level I, Level II includes aggressive encounters, singing, displaying, and so on. Priority Level III adds reproduction to the costs of the preceding levels. Utter (1971) proposes that the DEE required for egg production and feeding young ranges from 2.4 to 4.0 times BMR. This is in accord with the estimate of King (1973) that the DEE/BMR ratio is about 2.8 in domestic fowl during egg laying (see also Table 5), and with the data of Custer and Pitelka (1972) indicating that this ratio is about 4.0 in female Lapland Longspurs.

Utter's hypothetical model thus requires successively higher ranges of energy output for self-maintenance ($DEE/BMR = 1.2-2.1$), maintenance of social structure (1.6-2.6), and reproduction (2.4-4.0). The lower limit of Priority Level I in this model is probably too low (cf., Tables 3 and 4), but this may be regarded as a matter of opinion at this stage. Utter proposes that the ranges of overlap in the priority levels are of major ecological interest, since it is at these interfaces that an individual (or a species) can reach the next higher success level with the least expenditure of energy. This in turn is determined by environmental attributes (e.g., food, shelter, nesting substrate) and the individual's behavioral plasticity in optimizing the exploitation of these resources. "Optimizing" in this context means obtaining adequate resources with minimal time and (or) energy expenditure. At this juncture we return to a recognition of the detailed interaction between time budgets and energy budgets. A bird's energy intake (and the priority level attained) is directly proportional to time spent in foraging, although the proportionality is probably not linear (Schoener, 1971). The time available for nonforaging activities is obviously the reciprocal of foraging time. Hence, even though a bird may obtain the energy required to support the activities in a given priority level, it may not have enough time to

engage in these activities (e.g., space defense, courtship, nest building, and so on). The foraging efficiency, or what Utter (1971) calls "foraging fitness," thus has a prepotent role in determining whether a species can or cannot survive in a given environment. This theme is extensively developed by Schoener (1971), together with important ramifications that extend beyond the scope of the present account.

Seasonal Variations in Total Daily Energy Expenditure and in Time and Energy Budgets.—At this point we arrive at the current frontier of exploration of time and energy budgets. Very few comparative data are available as yet, and are confined almost entirely to a few species of land birds. Estimates of the energy requirements during various phases of the breeding cycle are available only from Mockingbirds and Lapland Longspurs. The daily energy expenditure of male Mockingbirds in New Jersey, estimated from time-activity data, was nearly the same in all phases of the nesting cycle, averaging about 28 kcal/day and ranging from 26.4 to 31.4 kcal/day. This conclusion is supported to a limited extent by a few concurrent measurements of D_2O^{18} metabolism (Utter, 1971). In contrast, Custer and Pitelka (1972) estimated, also from time-activity data, that the daily energy expenditure of Lapland Longspurs in northern Alaska was much more variable during the nesting cycle, ranging in males from a maximum of about 40 kcal/day during the courtship period to 25 kcal/day during the fledging and postfledging periods, and ranging in females from maxima of 30-33 kcal/day during the egg-laying and fledging periods to a minimum of 20 kcal/day midway through the incubation period.

Beyond this point we are dependent on time-activity budgets (Table 6) to illustrate the ranges of differences to be expected (in this very limited sample) among species, between sexes (e.g., Yellow-billed Magpie, Lapland Longspur), and through time within species (e.g., Mockingbird, Rufous-sided Towhee, Lapland Longspur). For additional examples, including fragmentary data from the nonbreeding season, see Gibb (1954, 1956), Orians (1961), Murton, Isaacson, and Westwood (1963), Verbeek (1964), Morton (1967), Root (1967), Goss-Custard (1969), Wiens (1969), Bock (1970), and Heppleston (1971). The components of time-activity budgets, owing to the different caloric equivalents of various activities, are only roughly proportional to the components of energy budgets (Stiles, 1971; Hainsworth and Wolf, 1971; Custer and Pitelka, 1972), and time budgets can be used only as limited approximations of energy budgets. Anna's Hummingbird (*Calypte anna*), for instance, uses 8.4% of its daylight hours but 17.7% of its daytime energy expenditure feeding at flowers on 21 June (Stiles, 1971). Assuming for the present, for lack of a better alternative, that the caloric equivalents of various activities are nearly the same among species and within species through time, the time-activity budgets (Table 6) provide some comparative insights that are not yet available through energy budgets. Conspicuous generalizations include the relatively small time spent in flight, except in aerial feeders

such as swallows, during the breeding season; the relatively small amount of time used in intra- and interspecific aggressive encounters; and the great variability among species in the amount of time spent foraging or resting. Foraging time, intensity, and strategy are, of course, influenced by air temperature (Verbeek, 1964) and substrate temperature (Goss-Custard, 1969), by thermal radiation (M. L. Morton, 1967), by daylength (Heppleston, 1971; M. Owen, 1972), by body size (Gibb, 1954), by the quality, quantity, and distribution of food supply (Morton, Isaacson, and Westwood, 1963; Heppleston, 1971; Wolf and Hainsworth, 1971), by reproductive events (Table 6; see, also, Root, 1967), and by sex roles and social attributes already mentioned. It is probably the mandatory feeding time, as the component of the time-energy budget most susceptible to the influences of phenotypic traits and extrinsic variables, that most strongly affects the allocation of time and energy to other categories and accounts for a major share of variability in the budgets. Food supply must therefore play a prominent role in time and energy allocation. The investigation of Rufous-sided Towhees (*Pipilo erythrophthalmus*) by Greenlaw (1969) appears to be the only one that has examined this possibility empirically and extensively in contrasting habitats. The data (Table 7) show that in an oak-hickory forest affording a greater density and diversity of food, Rufous-sided Towhees generally spend less time feeding and more time in reproductive activities than they do in pine-oak scrub affording lesser food resources. This difference was accompanied by a greater clutch size early in the season in the richer environment, but by about the same fledging success in the two. The towhees in the richer environment thus invested more in reproduction both behaviorally and physiologically and obtained a relatively smaller return on their investment, raising an interesting parenthetical question about which of the two environments was the "better" one. (The answer obviously depends on the criteria used.) The detailed interpretation of the data is confounded by differences of the population density of towhees in the contrasting environments (Table 7), and no doubt by factors (predation, interspecific competition) that were not quantified; but the essential point is the demonstration of intraspecific differences in the time budgets (and no doubt energy budgets) that are plausibly explained in part by differences in the trophic characteristics of the environments. In a similar investigation of Mockingbirds in two apparently less contrasting environments, Utter (1971) found several statistically significant differences in behavioral repertoires, but these were conspicuous only in the foraging time and singing time of unmated males.

The levels of energy expenditure by free-living birds outside the breeding season or summer season, and in particular the annual variations of the energy budget, are almost unknown. It is only the pioneering investigation by Kendeigh (1973) that has attempted to piece together, by extrapolations from laboratory measurements of existence

TABLE 6
Selected examples of time-activity budgets.¹

Species, sex, conditions	Percent of day or observation period spent in activities ²						Source
	Foraging	Flying	Preening, resting	Terr. defense, intersp. aggr.	Incubation	Singing	
Anna's Hummingbird, ♂♂							Stiles, 1971
Breeding territory: 21 Jan.	10	13 ³	81	6	---	---	
22 Mar.	9	12 ³	80	8	---	---	
Feeding territory: 5 Sept.	15	16	82	2	---	---	
Yellow-billed Magpie ⁴ : Males	72	6	20	1	---	---	Verbeek, 1972
Females	42	5	10	1	41	---	
Purple Martin ⁵ : Males	---	47	---	---	---	---	Utter and LeFebvre, 1973
Females	---	67	---	---	---	---	
Mockingbird, ♂♂ ⁶							Utter, 1971
Unmated	32	6	---	---	---	40	
Pre-incubation period	53	6	---	---	---	15	
Incubation period	25	7	---	---	---	7	
Nestling period	28	6	---	---	---	1	
Fledgling period	51	10	---	---	---	4	
Rufous-sided Towhee, ♂♂ ⁷							Greenlaw, 1969
Pre-Incubation period	64	3	---	---	---	4	
Incubation period	39	2	---	---	---	40	
Nestling period	83	2	---	---	---	3	
Fledgling period	66	2	---	---	---	11	
Post-fledgling period	41	2	---	---	---	50	
Dickcissel, ♂♂ ⁸	20	10	10	1	---	51	Schartz and Zimmerman, 1967
Savannah Sparrow, ♂♂ ⁹	24	4	8	3	---	61	Wiens, 1969
White-crowned Sparrow, ♂♂ ¹⁰	20	1	15	---	---	49	Lewis, 1974

TABLE 6 (continued)
Selected examples of time-activity budgets.¹

Species, sex, conditions	Percent of day or observation period spent in activities ²						Source
	Foraging	Flying	Preening, resting	Terr. defense, intersp. aggr.	Incubation	Singing	
Lapland Longspur:							Custer and Pitelka, 1972
Egg-laying period: Males	49	18 ¹¹	33	---	---	---	
Females	80	3	20	---	---	---	
Incubation period: Males	42	15 ¹¹	43	---	---	---	
Females	19	2	---	---	79	---	
Nestling period: Males	31	7 ¹¹	62	---	---	---	
Females	56	4	---	---	40	---	
Postfledgling & molt: Males	47	4	49	---	---	---	
Females	60	4	36	---	---	---	

¹ Heterogeneous data arbitrarily summarized in some cases and rounded to the nearest whole number for purposes of simplification in comparison. Vacant data cells signify either nil values or no observation in the activity category. In all cases consult the original references for an exact interpretation.

² Categories do not sum to 100% in most cases owing to omission of activity categories included in the original analysis.

³ Includes flying while foraging, hence categories sum to more than 100%

⁴ Averages for all phases of the breeding period.

⁵ Nestling stage of the breeding period.

⁶ Hopewell sample population.

⁷ Hutcheson Memorial Forest sample population.

⁸ Averages for all phases of the breeding period.

⁹ Averages for summer period.

¹⁰ Averages for males establishing breeding territories before arrival of females.

¹¹ Including song flights.

TABLE 7
Time budgets of male Rufous-sided Towhees related to variables in two habitats (data from Greenlaw, 1969).

Biotope	Food density	Utilized territory	Males per 100 acres	Clutch size ¹	Fledging success ²	Time budget, 1967 ³					
						Preinc.		Inc.		Nestl.	
						F	R	F	R	F	R
Oak-hickory forest (closed, mesic)	Greater	Smaller	21	4.2 (3.1)	1.9	64	22	42	43	82	3
Pine-oak scrub (open, xeric)	Lesser	Larger	32	2.8 (3.4)	2.5	89	3	70	20	74	12

¹ Early nests (late nests in parentheses). Differences significant ($P < 0.001$) between early clutches but not late clutches.

² Difference between areas not statistically significant.

³ Percentages of observation time spent in foraging (F) or reproductive activities (R, singing, courtship, and territorial defense) during the preincubation, incubation, and nestling periods. Data combined and transcribed from original categories, making it impossible to provide tests of statistical significance.

metabolism and other variables, the energy budget of a free-living bird. This model, in addition to depicting the energy outputs in various major functions, estimates that the daily energy expenditure of the House Sparrow in Illinois undergoes an annual cycle having a minimum (19.9 kcal/day) in August at about the onset of the molt, and a maximum (27.9 kcal/day) in midwinter. It remains to be shown whether or not an annual cycle of such amplitude is typical of House Sparrows and other resident birds that are free to engage in behavioral thermoregulation (Weiner, 1970), and whether or not migratory species also experience an annual variation of energy requirements. For instance, the metabolizable energy intake was nearly stable throughout the year in Willow Ptarmigan kept in large cages in essentially natural conditions of photoperiod and environmental temperature in central Alaska, in spite of the variable demands of molt, egg laying, and thermoregulation in environmental temperatures that varied from averages of -30°C in January to 14°C in June, and daylengths that varied from about three hours to nearly 24 hours (West, 1968). Likewise, Dolnik's (1971b) model of the energy budget of a hypothetical migratory bird estimates that daily costs are nearly stable through the year. (See, also, Davydov [1972] for a comparison of summer and winter energy budgets in European Starlings.)

The stability of energy intake on a seasonal scale observed in the Willow Ptarmigan resembles that estimated for several species of free-living rodents (Górecki, 1968, 1971; Trojan and Wojciechowska, 1969), including some inhabiting subarctic regions (Grodziński, 1971). In contrast, three species of dormice (excluding hibernating individuals) had a slightly to substantially lower energy requirement in autumn than in spring (Gebczyński, Górecki, and Drożdż, 1972). The daily energy expenditure of free-living *Perognathus formosus*, estimated by two independent methods, likewise undergoes a strong annual cycle with a maximum in winter in spite of reduced above-ground activity and a predilection for torpor during that season. White-tailed Deer free-ranging in an outdoor enclosure in New Hampshire also showed an annual cycle of voluntary food intake and fasting metabolic rate (Silver, Colovos, and Hayes, 1969), but with a minimum in winter.

Additional examples of annual variation in energy requirements could be cited, but would serve merely to substantiate the conclusion that the only generalization visible at this stage is that some species apparently undergo seasonal or annual variation of energy expenditure and others do not. This distinctly uninteresting assertion may serve a good purpose, at least, in diluting the widespread assumption that what we call "energy-demanding processes" (without really knowing much about them in an ecological context) are always additive and that, for instance, life in winter always costs a homeotherm more than life in summer. Seasonal or annual variations in energy consumption may be minimized (1) by behavioral adjustments that are impossible to study in the laboratory and difficult to discern in the field, and

hence remain largely unknown, (2) by compensatory reduction of energy expenditure in some categories as the demands of others increase, and (3) by temporal separation of energy-demanding processes in the annual cycle, as is typical of avian species inhabiting even allegedly stable tropical environments. Indeed, it is an interesting hypothesis (uttered *sotto voce*) that natural selection has tended to minimize seasonal variation in daily energy expenditure, perhaps stabilizing it as short-term oscillations around average allometric levels, as suggested by Figures 2 and 3.

SUMMARY AND CONCLUSIONS

We began with the assertions (1) that the concept of the annual cycle in its ultimate extensions subsumes all life-history phenomena, viewed in a temporal framework, (2) that supplies of time and energy are major selection pressures in the evolution of annual cycles, and are the single most important common denominator for recognizing and explaining adaptive strategies, and (3) that the group-specific patterns in the annual cycle represent optimal solutions of the problems of allocating time and energy resources to the requirements of self-maintenance and reproduction. These perspectives help to supply coherence and scope to subjects that are otherwise separated in the domains of physiology, ecology, ethology, and demography. We have seen that the annual cycles and other life history phenomena of birds do indeed include many elements that are plausibly explained as adjustments to the characteristics of time and energy resources. However, the absolute and relative amounts of these resources are affected by a staggering array of interacting biotic and abiotic variables, and the step from plausible explanation to reasonable proof can be taken only with the assistance of detailed investigations of the energy budgets, time budgets, and allied life history elements of birds in their natural microhabitats. Laboratory methods and controlled investigations will be a necessary part of this effort, but are not by themselves sufficient to produce realistic results. Major challenges to future students of avian ecological energetics will be to devise analytical methods that can be applied in the field, and to venture out more often from the comfort and convenience of their laboratories. In an era in which many areas of ecology are tending away from reductionism, it may seem wrong-headed to recommend an emphasis on more and better empirical data. Various forms of synthesis (modeling) will eventually be able to assist in coping with the complexities of the subject matter (and already have, in important but limited ways); but it is premature to expect that models of the time or energy budgets of various life history phenomena can be more than essentially undiluted speculations at present. At the end of the foregoing essay we arrived at a horizon depleted of data, but still nearly devoid of guideposts that might aid in formulating hypotheses (models) about the patterns and priorities by which birds allocate time and energy to essential functions. We can

begin to discern patterns only if we have more data. This means that we need at least (1) data defining avian microhabitats in physical terms, (2) data defining the physiological coupling of birds with micrometeorological factors, (3) data defining the energy costs of activities such as walking, hopping, preening, singing, and so on, (4) data defining the energy costs of productive processes such as molt, growth, and ovogenesis, (5) data defining the time-activity budgets of species with diverse life styles, and in central and peripheral parts of their ranges, and (6) data quantifying the effects of competition and predation in terms amenable to use in energy budgets.

As these and other, no doubt unforeseen, forms of information become available through the joint efforts of physiologists, ecologists, ethologists, and students of population biology we will begin to have the bits and patterns for the creation of models that will give us better insights into the ways that the temporal and social organization of bird species and communities reflects evolutionary compromises in the allocation of time and energy.

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DISCUSSION

WILLIAM R. DAWSON: I think that in view of the distinguished years which he has invested in topics which are particularly germane to this paper, I would like to call on Dr. Kendeigh first to give you some of his views, which are not necessarily coincidental with those of Dr. King. I shall, therefore, turn the arena over to Dr. Kendeigh.

S. CHARLES KENDEIGH:¹ Dr. King has given an excellent comprehensive review of the annual cycle of birds, the energy needs for accomplishing these activities, physical and biological factors affecting the energy budgets, and ways in which the energy budgets may be determined. I admire Dr. King's thorough knowledge and command of the literature. There are some points in his presentation, however, that need further clarification.

Basal metabolism.—I am unenthusiastic about the use of basal metabolism as a reference level for indicating energy cost of various activities. Jim defines basal metabolism as the rate of energy utilization of "birds resting without food at night in a thermoneutral environment". To say, for instance, that "the difference between exercised and sedentary" White-throated Sparrows, *Zonotrichia albicollis*, is $2 \times$ BMR is unrealistic. If we take 6.1 kcal/bird-day as the BMR of this species, then the metabolic rate of exercised birds will vary, dependent upon the temperature to which they are exposed, as follows, 35°C— $2 \times$, 30°C— $2.4 \times$, 20°C— $3.1 \times$, 10°C— $3.9 \times$, 0°C— $4.7 \times$. At all temperatures below 35°C, the difference is greater than $2 \times$ because of the requirements of body temperature regulation, and a correction for this factor must also be added to BMR to get the metabolic rate of exercising birds. Furthermore, the cost of a unit (M = kcal/bird-day) amount of exercise in this species varies with temperature (t) as $M =$

¹ For the convenience of the reader, Dr. Kendeigh has elaborated upon his oral presentation and also included references to pertinent literature.—Ed.

$28.75 - 0.48t$ (Kontogiannis, 1968). It seems to me a better goal to determine the energy cost of various activities in absolute terms than to relate it simply to BMR.

Cage activity.—I am concerned with Jim's criticism of our measurements of existence metabolism in that they do not take into account differences in locomotor activities of the caged birds at different ambient temperatures. He points out that in some species this cage activity greatly increases at high ambient temperatures and therefore the temperature coefficient of existence metabolism for these species should be lower than in species that do not become more active at high temperatures. Because of these behavioral differences between species, existence metabolism, as we have been measuring it, has no exact comparative value nor does it furnish a good basis for calculating productive energy available for other activities. This criticism needs to be answered, as we have found the concept of existence metabolism a very useful one, and measurements of it, as I will show later, come closer to values of total metabolism of free-living birds and furnish a better basis for calculating daily energy budgets than does standard metabolism and certainly a much better basis than does basal metabolism.

Cage activity has been measured, along with existence metabolism, in several of our experiments. Although reported in our publications, we have not placed great emphasis on the quantitative measurements of activity because of skepticism concerning their accuracy. Activity was measured by a perch and false cage bottom suspended from a microswitch. The number of activity units registered depended on the bird hitting the perch or bottom in its movements around the cage. Hopping from wall to wall or to top of cage were not recorded. Different individual birds developed different patterns of movements within the cage and varied in the frequency with which they alighted on the perch or bottom. Variations in movement pattern even occurred in the same individual at different times. However, the data do indicate a difference in amount of activity of some species at different temperatures even if they may not be exact measurements of this activity.

Since the unit of activity used has varied in the study of different species, the amount of activity at various temperatures has been put in terms of percentage of the mean activity at all temperatures. Total cage activity in the House Sparrow (*Passer domesticus*), White-throated Sparrow (Eyster, 1952, 1954), and Redpolls (*Acanthis flammea*, *A. hornemanni*) (Brooks, 1968) at two different photoperiods definitely increases at higher ambient temperatures, but no significant variation occurs in the Field Sparrow (*Spizella pusilla*) (Olson, 1965), Dickcissel (*Spiza americana*) (Zimmerman, 1965), and Slate-colored Junco (*Junco hyemalis*) (Eyster, 1952, 1954) (Fig. 1.). This is daytime activity that is analyzed, to avoid the complications of nightly unrest that occurs at certain times in migratory species.

Cage activity probably has three components. (1) Feeding movements, that is, hops to the food container and back again, although

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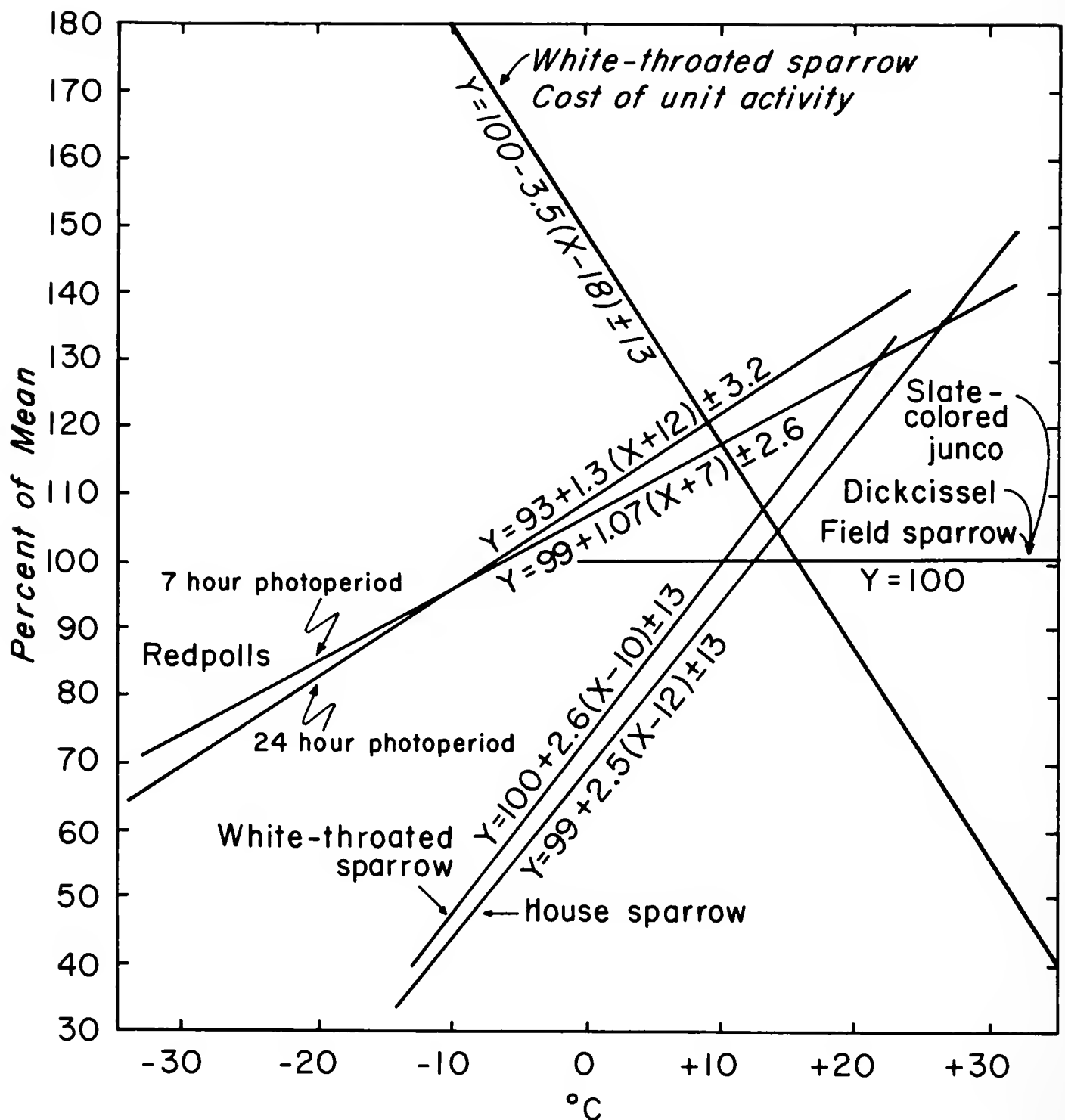


FIG. 1. Regression of locomotor cage activity on ambient temperature.

not separately measured, presumably increase at lower temperatures proportional to the increase in food consumption. On the other hand, (2) hops back and forth to the water container presumably increase at high temperatures. The activity involved with drinking, however, is probably very small. The increase in total activity at high temperatures must be due (3) to what may be called *frivolous* activity, that is, locomotor movements that serve no apparent useful function but appear the outlet simply of nervousness, uneasiness, or surplus energy. In the House Sparrow, White-throated Sparrow, and the two Redpolls, the increase of this frivolous activity more than compensates for the decrease of movements involved in feeding. In the Field Sparrow, Dickcissel, and Slate-colored Junco the increase in frivolous activity at high temperature equals the decrease in feeding activity so that total activity is nearly uniform at all temperatures. Frivolous activity

may also occur in free-living birds, but we have no direct measurement of it nor how it may vary with ambient temperatures.

Variations in cage activity do not constitute an accurate index of the amount of energy being spent in that activity, however. Kontogianis (1968) has shown for the White-throated Sparrow that the cost of a standard unit of forced activity increases from 40% of the mean at $+35^{\circ}\text{C}$ to 180% at -10°C . The temperature coefficient for this increased cost ($-3.4\%/^{\circ}\text{C}$) is higher, although of the same order of magnitude, than the coefficients of activity ($+1.07$ to $2.69/^{\circ}\text{C}$). It is quite possible that the increased activity evident at high temperatures in the House Sparrow, White-throated Sparrow, and Redpolls does not cost, energywise, any more than does the lesser activity at low temperatures. Adjustment to tolerate low ambient temperature may well involve reduction of frivolous activity.

I do not know why the Field Sparrow, Dickcissel, and Slate-colored Junco show no consistent change in cage activity with temperature. It may be due to some change of movement pattern within the cage, as above mentioned. It is significant that the temperature coefficient of existence metabolism for these three species fall in line with the other species that show change in activity with temperature (Table 1).

Heat increment of feeding.—Another complicating factor in the concept of existence metabolism that Jim might have mentioned but did not, is the specific dynamic action or the heat increment of feeding. Within the zone of thermal neutrality, all the heat generated in the assimilation of food is lost from the body without serving any useful function. At low temperatures, as gross energy intake increases, there is, of course, a corresponding increase in the amount of heat generated. Below the zone of thermal neutrality, progressively larger amounts and eventually all of this heat is retained for temperature regulation, thus reducing by that much the increased tissue metabolism that would otherwise be required. This is Rubner's (1910) Law of Compensation.

Existence metabolism is thus not a simple physiological function comparable to basal or standard metabolism but involves a number of processes: basal metabolism, tissue heat production for body temperature regulation, heat increment of feeding retained for temperature regulation, heat increment of feeding lost from the body, and locomotor behavior. These same processes occur in wild birds and doubtlessly vary at different temperatures in a similar manner. Because of this integration of factors, the concept and measurement of existence metabolism is of considerable ecological importance, both theoretically and for application to the activities of birds under natural conditions.

Molt.—Jim makes a good point that reduction in cage locomotor activity during molt may be a factor that reduces the total energy expenditure at this time. There is no doubt that the molting process requires a considerable amount of energy. Blackmore (1969) shows this clearly by using a complex computer program that eliminates the increasing insulation and conservation of energy provided by the new

TABLE 1
Comparative Effect of Ambient Temperature on Existence Metabolism and Activity (in part from Kendeigh, 1970).

Species	Photoperiod (hours)	Weight (g)	Coefficients		Activity %/°C
			existence metabolism kcal/bird-°C-day	metabolism kcal/g-°C-day	
Dickcissel, <i>Spiza americana</i> , ♂	10-15	31.6	-0.527	-0.017	0
Dickcissel, <i>Spiza americana</i> , ♀	10-15	29.6	-0.532	-0.018	0
White-throated Sparrow, <i>Zonotrichia albicollis</i>	10	27.4	-0.380	-0.014	+2.6 (14 hours)
House Sparrow, <i>Passer domesticus</i>	14-15	25.2	-0.320	-0.013	+2.5
Slate-colored Junco, <i>Junco hyemalis</i>	10-15	19.4	-0.208	-0.011	0
Redpolls, <i>Acanthis</i> sp.	7	14.5	-0.235	-0.016	+1.07
Redpolls, <i>Acanthis</i> sp.	24	14.3	-0.332	-0.023	+1.3
Field Sparrow, <i>Spizella pusilla</i> , ♂	10-15	13.9	-0.290	-0.021	0
Field Sparrow, <i>Spizella pusilla</i> , ♀	10-15	13.2	-0.274	-0.021	0

plumage as it develops. The full value of the savings in energy is evident by comparing the levels of existence energy for the weeks preceding the onset of molt and following its completion. It is quite likely that the savings in energy expenditure while molt is in progress is not due entirely to the better insulation of the new plumage, as we have supposed, but in part also to the decrease in activity at this time that has been shown to occur (Eyster, 1954). Since this reduction in activity during the molting period also occurs under free-living conditions, this is another demonstration of the importance of metabolized and existence energy as useful indices of what occurs in nature, even though because of the behavior factor involved, the physiological interpretation of what is taking place is complicated.

Daily energy budget.—I am particularly interested in Jim's attempt to get an equation for calculating the daily energy budget (DEB) ($M = \text{kcal/bird-day}$) for any species knowing the weight of the bird. This equation, using $W = \text{grams}$ instead of kilograms, is:

$$\log M = 0.3864 + 0.7052 \log W$$

I have also derived equations for calculating DEB of various species, specifically granivorous passerine birds, using quite a different procedure that requires the measurement and adding together each month, as appropriate, the energy costs of cage existence, locomotor free existence activity, reproduction, molt, and weight change. These equations are based on our work with the House Sparrow, but the procedure on how they are derived is too long and complicated to review here (Kendeigh, 1973a,b). It is necessary to note, however, that different equations are given for the nonbreeding season (November through April) and the breeding-molting period (May through October), and that they incorporate the ambient temperature factor.

During the nonbreeding season, DEB was found to average about 107% of existence metabolism, as determined by calculations made for the House Sparrow at seven localities extending from Churchill, Manitoba to Tucson, Arizona, and Vero Beach, Florida. If we assume that DEB varies with the weight of birds not as does basal metabolism, which is very unlikely, but as does existence metabolism, then our equation for the relation of existence metabolism to bird weight (Kendeigh, 1970) may be corrected for DEB (M) as follows:

$$(30^{\circ}\text{C}) \quad \log M = 0.2259 + 0.6210 \log W$$

$$(0^{\circ}\text{C}) \quad \log M = 0.6669 + 0.5300 \log W$$

During the *breeding-molting season* the percentage (PC) DEB of existence metabolism is not constant but varies with temperature in the House Sparrow as follows:

$$\text{PC} = 132.7 - 0.929t$$

Thus at 30°C , DEB is only 104.8% of existence metabolism; at 0°C it is 132.7%. Using these percentages the equations for DEB become:

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$$(30^{\circ}\text{C}) \quad \log M = 0.2168 + 0.6210 \log W$$

$$(0^{\circ}\text{C}) \quad \log M = 0.7601 + 0.5300 \log W$$

When DEB at two different temperatures are known for any species, it is a simple matter to calculate an equation showing how it varies with temperature in that species.

These equations are only first approximations. Very likely the regression equation for DEB on weight is not the same as for existence metabolism. I suspect, when studies have been made on a variety of species, it will be found to be smaller although possibly not significantly so. Furthermore, Dr. Charles Blem and I have recently found that the level of energy metabolism is adapted to local climate, being higher than expected at northern localities, lower than expected at southern localities. We have a correction equation for the House Sparrow for adaptation to local climate but not for other species (Kendeigh and Blem, 1974).

There have been a few attempts, as Jim mentioned, to estimate DEB by use of time-activity budgets and doubly labelled water. With time-activity budgets, it is necessary to establish the energy cost of each activity. Schartz and Zimmerman (1971), working with the Dickcissel, estimated activity costs as multiples of existence metabolism but, in comparison with my equations, obtained values some 18% too high (Table 2). Likewise, my estimates for DEB of the Purple Martin are considerably lower than those of Utter and LeFebvre (1973) with either the time-activity budget or the use of doubly labelled water. On the other hand, Custer and Pitelka (1972), when they add a correction for body temperature regulation, obtain values for the Lapland Longspur that are reasonably close to my estimates.

I hope that the time-activity budget procedure for estimating DEB can be perfected to a reasonable degree of accuracy. It is a field method requiring a minimum of equipment, does not require capturing the bird, and is applicable to a variety of situations all over the world. However, there are many difficulties in its use and many variables are involved. Very critical at the present time is the neglect of the temperature factor which largely determines the energy requirements for existence before any other activity can be performed at all. Existence metabolism calculated for the prevailing ambient temperature, is a better base to relate the energy cost of various activities than is basal metabolism. Corrections should be made for energy conserved by roosting sites, time spent exposed and not-exposed to solar radiation, influence of the wind, etc. Jim is quite correct that birds in their micro-climate are often exposed to conditions not reflected in the statistics of the macro-climate. Attention must also be given to changes both in the micro-climate and in the physiology of the bird with the season of the year. All in all, the method is complex and full of pitfalls but is not unsolvable.

Of course, it is highly desirable to develop energy budgets by direct

TABLE 2
Comparison of Daily Energy Expenditures (DEB=kcal/bird-day) During Breeding Season, Calculated by Different Methods.

Species	DEB		Kendeigh equations				King equation	
	Time-activity budget	D ₂ O ¹⁸	Temp.	Weight	DEB	Per cent differences	DEB	Per cent differences
Dickcissel ¹ Male	24.4	---	(21.8°C)	(31.6g)	20.0	-18.0	27.8	+13.9
Purple Martin ² Male	38.5	32.7	(20±)	(51.8)	28.3	-26.5	38.4	0
Female	44.2	41.9	(20±)	(50.0)	27.7	-37.3	37.3	-15.6
Lapland Longspur ³ Male	38.0	---	(-1.9)	(28.0)	35.0	-7.9	26.0	-31.6
Female	35.2	---	(-1.9)	(29.0)	35.6	+1.1	25.9	-26.4

¹*Spiza americana*, Schartz and Zimmerman, 1971.
²*Progne subis*, Utter and Le Febvre, 1973.
³*Calcarius lapponicus*, Custer and Pitelka, 1972, later revised (pers. comm.).

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measurement, as our group has done for the House Sparrow, and by the use of doubly labelled water or bio-telemetry (Gessaman, 1973). When complete measured budgets have been obtained for several species, then more reliable equations can be formulated for prediction purposes than the preliminary ones that I have presented.

The use of D_2O^{18} holds great promise. The method is still in its developmental phase, however, and needs to be tested thoroughly with values obtained by other procedures. The values shown in Table 2 for the Purple Martin are quite different from those I have calculated. Of course, mine may be wrong in not allowing enough energy cost for the extensive flying by this species—but whether or not this is necessary is uncertain (see discussion, p. 71). The use of doubly labelled water has a disadvantage in that the bird must be captured for injection of the isotopic hydrogen and oxygen and later for securing blood samples. The value obtained for energy use is an integration for all activities during the interval.

The development of telemetry should also be pursued. With telemetry the bird carries a transmitting device that may modify its activities but has the advantage that different activities of the bird cause the equipment to emit different signals that can be translated into energy units for that activity. Heart rate is commonly used as the indicator of the rate of energy use, and, of course, this must be interpreted with care.

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DR. DAWSON: I'd like now to call on Dr. Odum. One of the major thrusts in the last five or six years, as many of you know, has had to do with ecosystem modelling and with the modelling of ecological systems in general. Dr. Odum has been very actively interested in this. Fundamentally, what one would like to do in science, of course, is to develop some predictive relationships. This is somehow particularly pertinent to certain of the things we're talking about here, which really strike at the essence of avian life histories and so on. I've asked Dr. Odum if he would perhaps comment on modelling as it might apply to this, the obvious limitations that presently confront us, and, perhaps, the direction we might follow in relation to the very desirable goal of being able to attain predictability in analyses of avian biology.

EUGENE P. ODUM: Ornithology has moved progressively over the centennial span of the Nuttall Club from primary concern with inventorying the North American avifauna to more and more attention to analytical problems. Birds constitute highly desirable models for investigation of many aspects of behavior and ecology of broad interest beyond the field of ornithology, and energy became a central dimension in such studies. The well prepared review papers being presented here today are not only labors of love by the authors, but will constitute, when published, an important monograph. In commenting on the papers I shall not only try to bring out highlights, but also to relate avian research to the broader area of ecological energetics, a subject that will become of increasing concern to man.

There are several aspects of Dr. King's paper that I liked particularly. First, he showed us how one can begin to develop a predictive model from a simple graph. This is the way one would set up a cost-benefit model for man's as well as a bird's use of energy. However, because those of us living in the affluent countries have a total energy budget about 100 times that required for physiological needs, we can't depend on natural selection to keep us from going too far—to and beyond the point of diminishing benefits. In other words, the bird is under constant selection pressure to develop the best possible life style within the limits of available energy; man has been able to postpone seeking an equilibrium by exploiting concentrated energy sources, but

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sooner or later he will have to establish negative feedback to avoid negative selection. What I'm trying to say is that these models we're seeing for birds can be expanded and are very relevant to the total system of man and environment. In projecting from one level to another, however, there's one very important principle which everyone tends to forget. We call it the *principle of integrated levels*, which means when you put several components together, like bird species together to form a community, and then put these together with plants and other components to form an ecosystem, you add new properties, which in many cases are not predictable from models of the individual species or populations. Thus, what a bird really does may be determined by the nature of the system, such as type of food chain, or energy use by competitors, rather than by physiological adaptations within the species. Let's not be too reductionist like the biochemists and get more and more concerned with internal details and forget that the whole is not the sum of the parts. We all know this, but we tend to forget it in the pursuit of scientific specialization. For instance, the cost-benefit optimum, as shown in King's graphs, may or may not apply to the bird in nature. In the real world the optimum may be determined more by *other parts of the system*. There are many examples where species in nature do not live at their physiological optimum; some other property of the system may force a different interaction. In other words, the optimum may be shifted either to the left or to the right, depending upon the interaction of other organisms and other components in the system, you see, so you'll never be able to determine the optimum simply by studying one species at a time.

Now for the geographical aspect of King's models. The world consists of gradients from north to south with major changes in properties along the gradient. Unfortunately, most ornithology and most science is northern, and birds are viewed mostly as they are perceived in New England and so on. Thus, a bird migrates north, breeds, molts and then goes south, with appropriate allocations of energy in neat seasonal packages. Just because we know the northern model very well does not mean it applies everywhere. We might call this pattern the *bloom-type, seasonally programmed life history pattern*—where everything has to be done very quickly in a limited time span. The life history is timed to take advantage of brief but high energy outbursts. Energy allocations are very sharply determined and very easy to measure. But at the other end of the gradient, the tropics, there are longer, more spread-out, seasons. Breeding, molting, and other activities requiring extra energy may not be sharply separated and timing may be determined by biotic factors that don't operate on a rigid calendar schedule. Energy in the tropical system is more evenly distributed over the season with fewer "bloom" periods where a large storage of food, nutrients or other sources is available for quick exploitation. In other words, as one goes south the northern type energy budget is less and less appropriate.

Now, I am not enthusiastic at all about Dr. King's interest in micro-

climates. Plant ecologists went haywire over that 30 years ago and, as far as I know, they learned almost nothing about plant communities because this approach goes in the direction of greater and greater attention to instrumentation and the study of physiology of the individual. There is nothing wrong with this if one's aim is to move from ecology to physiology to biochemistry.

In summary, what I am saying is that study at any level of organization tells us something, but not everything, about that level. To fully evaluate the findings one must model at least one level lower and one level higher. Because of the reductionist nature of science we tend to take care of the lower level, but forget the next higher one. Thus, as I see it bioenergetics of birds is not only a matter of energy metabolism of individuals and species, but also a matter of the energetics of the ecosystem.

DR. DAWSON: Dr. Bartholomew has some brief comments. I should like, after he's concluded and before opening the discussion to the audience, to allow Dr. King, whom I've now worked into a position like that of Cyrano de Bergerac fencing with several people on the stairway, to respond as he so desires. Dr. Bartholomew.

GEORGE A. BARTHOLOMEW: It's a well-known attribute of important scientific insights that after they are first phrased by some pioneer, they seem like platitudes. I'm about to produce some insights that are platitudes even before I say them. The first of these platitudes, however, is one that needs to be uttered frequently and in a loud voice. The progressive increase of knowledge forces all of us, because of our limited capacities, into ever greater specialization. Although this situation is almost inevitable, it unfortunately results in an endless splitting of biology. The familiar subdivisions of behavior, genetics, physiology, morphology have become so fully institutionalized that they represent barriers that we must somehow or other break through. The only place where these unfortunate barriers are real is in the minds of university deans and department chairmen. For the animals artificially fragmented by these partitions, they do not exist; they are artifacts. For this reason persons such as you in this room are in a uniquely important position for the future of biology. Whatever your special interests, each of you studies organisms which integrate all these man-made subdivisions, and therefore you represent what can be the wave of the future in biology. If you follow an animal and try to understand it, you are forced to break through man-made partitions which distort the essential unity of biology.

DR. DAWSON: Dr. King, do you have any words of wisdom you would like to offer? Please, some words of wisdom!

DR. KING: Professor Odum's main assertions about my points of view, to the extent that I have been able to filter them from his lively

presentation, seem to be (1) that I advocate some retrograde form of reductionism, exemplified by (2) my overzealous preoccupation with the definition of avian microhabitats, and (3) that I have been insufficiently attentive to modelling as a synthetic process. The written version of my contribution addresses these subjects at greater length than was possible orally today, and so the present exchange may seem odd to subsequent readers. Nevertheless, a few points merit reiteration and emphasis. First, there is no question that the exceedingly intricate input-output relations that comprise the avian patterns of energy allocation will eventually be susceptible to the kinds of formalized treatment currently being called modelling. There is likewise no question that *a priori* modelling can assist us in recognizing and organizing profitable lines of investigation. In the world of hard science, this has always been called "the formulation of an hypothesis", and has not been regarded as a novelty since the era of Francis Bacon. The concept of emergent properties, mentioned by Professor Odum as "the principle of integrated levels", is likewise less than novel, having been much in vogue among the natural philosophers of the 19th century. Professor Odum and I converge in recommending continued attention to these principles.

Professor Odum cautions us against excessive reductionism, by which I assume that he means excessive concentration of attention on levels of interaction or organization below the levels at which the emergent and unique properties of living systems become evident. This is wise counsel. A glance at Figure 1 of my chapter will reveal that I am scarcely a partisan of unalloyed reductionism; yet Professor Odum obviously believes that my emphasis on analyzing the relation between an organism and its microclimate is overzealous, if not harebrained reductionism. This attitude is difficult for me to fathom. What Professor Odum seems to be advocating instead is a mode of investigation in ecological energetics that omits input from the individual organism and its particular environment. This can be viewed as a paradoxical form of neoreductionism in which the focus of investigation is reduced not to a point below the level of emergent properties, as in classical reductionism, but rather to simplifications that are no longer traceable logically or sufficiently to the biophysics or even the biology of the individual organism. Since it is widely conceded that natural selection acts on individuals rather than on other levels of biological organization, this cast of mind deprives investigation of the evolutionary perspective that is central to biological theory. Without this essential tether to the real world, it is all too easy, through the comforting formalities and conventions of modelling, to go twittering off into the ionosphere. It is with this hazard in mind that I have intentionally avoided more than the simplest of models and have strongly emphasized my opinion that it is too soon to forego empirical investigation of real birds in their real habitats. We need to know much more about them before physiological ecologists such as myself will regard auto-

ecological models with more than uneasy scepticism. It is true that we have already seen some interesting models of the energetics of avian communities, and perhaps the time is not far off when we can begin to work rigorously at the level of the individual and the species. I suspect that Professor Odum and I are not really very far apart in our opinions that this process will not be aided or hastened by forms of reductionism at either end of the spectrum.

I believe that I can respond productively to most of Professor Kendeigh's points, but first I prefer to set the stage by means of some general observations. In the context of our subject matter today, Professor Kendeigh is functioning as a laboratory-oriented ecologist and I am functioning as a field-oriented physiologist. It is no surprise to discern from Professor Kendeigh's remarks that some tensions and divergent interpretations exist between two such unorthodox disciplinary perspectives. I think that these tensions and exchanges are essentially salutary for progress toward our mutual goals, and should not be mistaken as astringent criticisms. Dialogue, tension, interchange of perspectives and skills, and criticism are especially pertinent here because of the unusually diverse disciplinary mix needed to cope with our mutual problems in a young and intricate field of knowledge. Such exchanges can help us to guard against premature conclusions and interpretations that are apt to become solidified as dogma when physiologists overzealously extrapolate ecological viewpoints, when ecologists uncritically adapt physiological data to their needs, when ethologists accept unwarranted compromises by both physiologists and ecologists, and so on. This is the framework from which the following specific reflections originate.

First, Charles has misgivings about my preference for the use of BMR as a base for comparing (or "normalizing" in statistical terms) various metabolic costs. He notes that it is "... a better goal to determine the energy cost of various activities in absolute terms than to relate it simply to BMR." We obviously are not understanding each other at this point, since it is impossible to relate an energy cost to BMR unless it has first been estimated in absolute terms. My preference for BMR instead of SMR, resting MR, existence MR, or other alternatives, originates mainly from statistical considerations. Among the various comparative bases that might be selected, the BMR is the best defined operationally, includes the least number of variables, and is the best established statistically as well as allometrically. In short, among the several alternatives, the error of estimate is least for BMR. This means that error is also minimized if BMR instead of an alternative is used as a common denominator in comparing data. Although they elude me at present, I concede that there may be cases in which it is useful to sacrifice statistical precision in favor of a comparative base other than BMR; but the quantitative effects of this compromise should not be overlooked.

Second, Charles responds at length to my queries about the inde-

terminate, or at least undetermined, effects of temperature-dependent locomotor activity on estimates of metabolizable energy expenditure as a function of air temperature in various species. My observations on this subject are not intended as an indirect attack on the concept of existence energy, which I believe has had an enduring catalytic effect on ecological energetics. I could readily be persuaded that error resulting from variation in locomotor activity is slight compared with other sources of error. Nevertheless, I have called attention to this problem because, to the best of my knowledge, it has not previously been addressed in the literature, and I do not really know that it can legitimately be ignored.

Third, I intentionally avoided discussion of the heat increment of feeding, as Professor Kendeigh notes, because I had nothing very useful to say about such a controversial subject. Evidence that has accumulated since Rubner proclaimed his "Law of Compensation" at the turn of the century shows that the heat increment of feeding seems to substitute almost fully for thermoregulatory calorigenesis in some species or settings, partially in others, and has no detectable effect in still others. The ecological significance of this process is therefore equivocal, or at least unpredictable at present, and I prefer to avoid assumptions that may mislead those who unknowingly rely on authority rather than evidence.

Finally, Professor Kendeigh has used my equation (for daily energy expenditure as a function of body weight in free-living birds) to compute values that he compares with parallel estimates based on equations for existence metabolism in caged birds and with estimates derived from time-activity methods and the D_2O^{18} method. The algebraic mean error (computed from data in Kendeigh's Table 2) is about -19% for estimates based on the Kendeigh equations and about -8% for estimates based on mine. This involves an element of circular reasoning, since my equation for birds includes the data for the three species whose daily energy expenditure it was used to estimate. The time-energy estimates for the Dickcissel are likewise based in part on the existence-metabolism equations. Nevertheless, our grossly similar results from essentially independent approaches represent a step forward by suggesting that we are both in the right ballpark quantitatively. This is less interesting than it might seem superficially, since the additive sources of error are relatively small compared with the potential range of variation of daily energy expenditure, which is itself rather narrow (as judged from investigations of domestic animals). In other words, it is predictable that even very tenuous independent estimates will differ by much less than an order of magnitude.

Professor Kendeigh believes that daily energy expenditure as a power function of body weight does not parallel BMR (as in my Fig. 2), but instead is a power function equal to (or less than) that for existence metabolism. I have no preconceived notions on this subject, and prefer to let the data speak for themselves. I have tried to emphasize in my

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earlier presentation that my equations are based on heterogeneous data spanning a range of body weight that is only marginal for reliable allometric analysis. I reiterate my belief that it is improbable (based on the statistical evidence now available) that additional data will alter the conclusion that average daily energy expenditure in free-living homeotherms parallels BMR as a power function of body weight; but I would be neither surprised nor dismayed to find that future evidence leads to a different conclusion. Personally, I would not use my DEE equations for making extensive predictions about any particular species. The equations seem too crude for this purpose, and overenthusiastic extrapolations from them may lead to unproductive substitutes for rigorous and penetrating analysis.

CONSEQUENCES OF BODY SIZE FOR AVIAN ENERGETICS

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INTRODUCTION

This topic was originally to have been discussed by the late Robert Lasiewski. Bob's contributions to the field of avian energetics were extensive, spanning the five orders of magnitude from hummingbirds to the rhea, emu, and ostrich (Lasiewski, 1962a,b; 1963a,b; 1964; Lasiewski, et al., 1967; Lasiewski and Lasiewski, 1967; Crawford and

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Lasiewski, 1968; Schmidt-Nielsen, et al., 1969). His research yielded valuable insight into the allometry of metabolism (Lasiewski and Dawson, 1967, 1969), thermal conductance (Lasiewski, et al., 1967), evaporative water loss (Crawford and Lasiewski, 1968), respiration (Lasiewski and Calder, 1971; Lasiewski, 1973), and heat stress (Lasiewski and Seymour, 1972). An all too brief collaboration with Bob was a stimulating and enjoyable experience for me, one that made me acutely aware of our loss when this dynamic biologist was no longer with us. I am sure that what he would have contributed to this symposium would have been more exciting than the following attempt.

I will begin with a review and analysis of the influence of body size on avian energetics. Then I will examine the specific problems and their implications for the smallest birds, hummingbirds (see Fig. 1).

IMPORTANCE OF BODY SIZE

There are about 8,656 species of living birds (Brodkorb, 1971). While it has been possible and necessary to describe, catalog, and show relationships between all of these, attempting to obtain metabolic rates for all 8,656 species would be highly impractical. For expediency, generalizations must be made from studies representing a smaller number of species but a variety in phylogeny, food habits, habitat, locomotion, and body size. From this it appears that body size has the greatest influence.

The consequences of size can be induced semiquantitatively from tables of data or graphs. However, the use of mathematical power functions is more compact than tables and more precise than graphs. For an example of such empirical descriptions, metabolic rates (\dot{H}_m) have been summarized as functions of body mass (m , in grams, or M , in kg):

$$\dot{H}_m = a M^b \quad (1)$$

in which the constant a characterizes a group of animals and the exponent b describes the effect of size within the group.

Linear equations are easier to handle, and such can be obtained by converting equation (1) to the logarithmic form:

$$\log \dot{H}_m = \log a + b \log M \quad (2)$$

The utility of such treatment has now spread to a variety of physiological, morphological, and ecological functions, stimulated by Kleiber (1932, 1961), Brody (1945), Adolph (1949), Zeuthen (1953), Hemmingen (1950, 1960), and Stahl (1967). Consequently, we can now obtain an extensive perspective on the influence of body size in the life-support of birds. Before proceeding with the analysis, it would be well to review graphically the meaning of the exponent.

Figure 2 is a graph of various hypothetical functions (Y) of body

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FIG. 1. Whatever the consequences of body size, they should be most evident in the natural history of the smallest birds. Faced by natural selection in hostile environments, the hummingbirds' success has depended upon effective energy conservation, such as nesting in places of reduced exposure and relying upon hypothermia in times of "energy crisis". Man would do well to "[re]consider the birds" as the time of natural selection against his profligacy draws nigh.

Woodcarving of the Broad-tailed Hummingbird's nest site by William A. Calder, IV.

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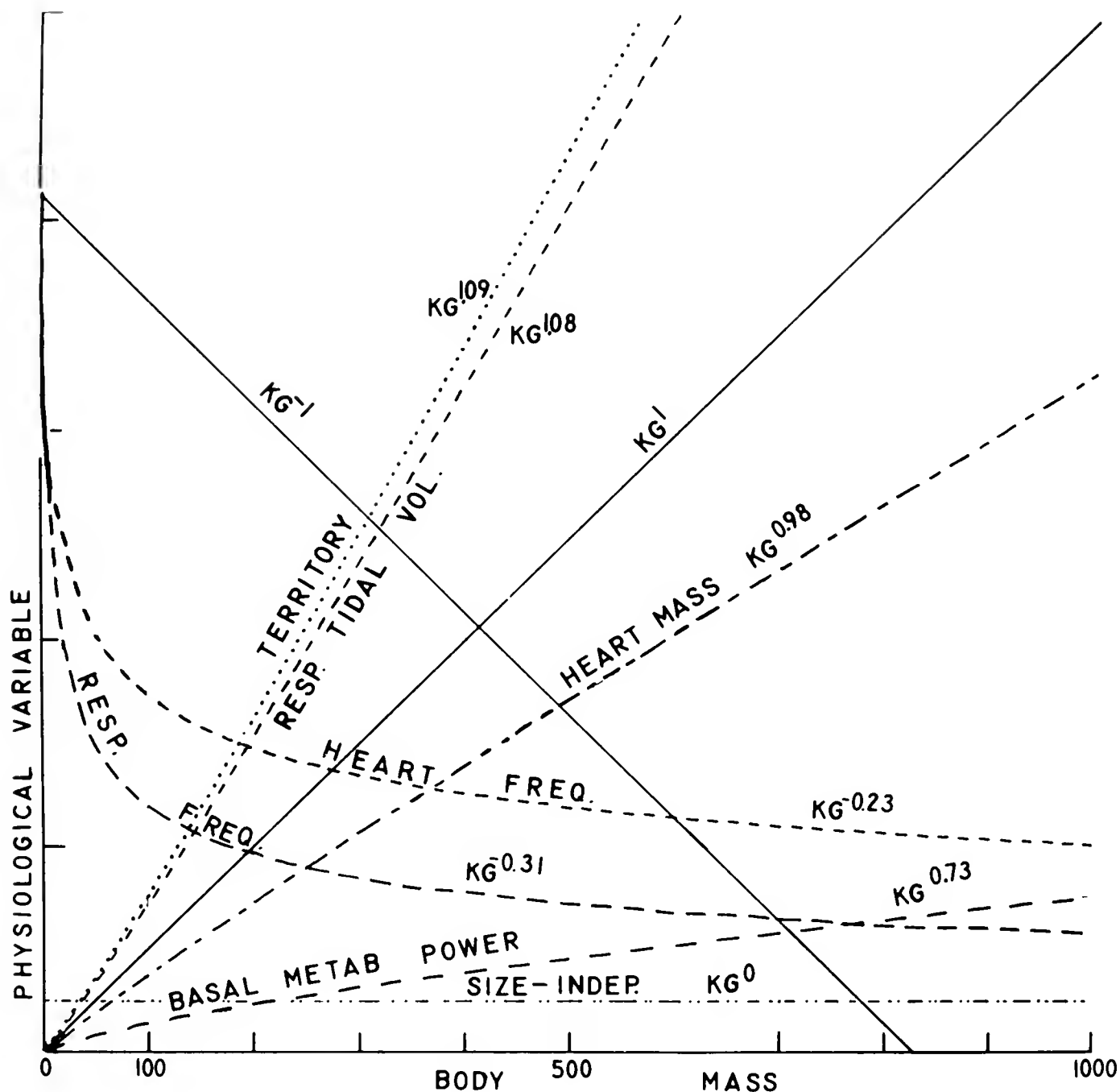


FIG. 2. Physiological and ecological functions of body mass [$y = a(kg)^b$] plotted on linear coordinates. Note that only the functions $kg^{1.0}$, kg^0 , and $kg^{-1.0}$ plot as straight lines. Modified from Zar (1968).

mass (kg). Following Zar (1968), we can see that there are five types of exponents:

- (1) Exponent = 1.0: linear increase in "Y" (capacity, volume, or weight of vegetative organs, not including control organs such as the brain and endocrine glands), e.g., a bird weighing ten times as much has ten times as much gut.
- (2) Exponent > 1.0: "Y" increases more rapidly than body mass, e.g., territory and home range of carnivores (Schoener, 1968).
- (3) Fractional exponent ($0 < \text{exponent} < 1$): the variable "Y" increases with body size, but progressively less so for each additional increment of body mass, e.g., metabolic rate, surface area, lifespan.
- (4) Exponent = 0: "Y" is a constant, independent of size, e.g., fractional utilization (inspired-expired % O_2).
- (5) Negative exponent: variable "Y" decreases with size, e.g., breathing and heart rates.

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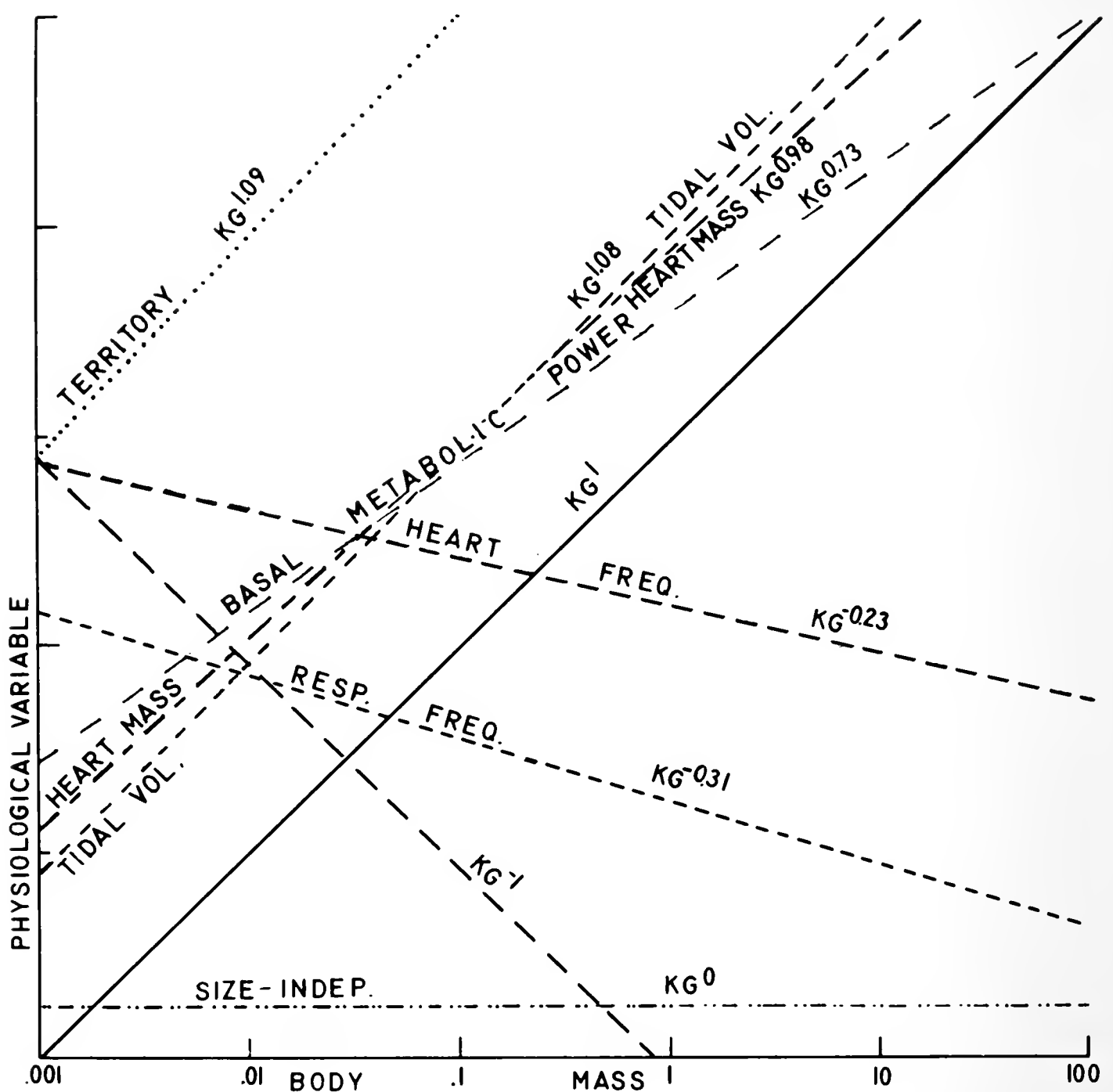


FIG. 3. The functions that were shown on linear coordinates in Figure 2 have been replotted after logarithmic transformation [$\log y = \log a + b \log(kg)$]. Now all are straight lines with slopes equal to the exponents before transformation. Modified from Zar (1968).

These functions are replotted on a log-log scale in Figure 3, making them all straight lines. Note that the linear and constant functions have the same slopes as they did on the linear-linear plots, and that the exponents are the slopes of the linear regressions.

Attempts to provide a theoretical basis for the exponent or log-log slope of well-established empirical expressions provided valuable food for thought, but the results had not been conclusive (see Kleiber, 1961; Hemmingsen, 1950, 1960). Recently, however, McMahon (1973) introduced arguments based on elastic stability and flexure (I shall review this below.).

Even without the physical reason for a particular slope, we can analyze the empirical descriptions for the interim goal of seeing a pattern set by whatever physical constraints are involved. Perhaps this is merely a game of numerical coincidences, but I think that there is

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more to it than mere coincidence, because of both internal consistency and parallel evolution. The internal consistency is seen when independently derived allometric expressions are substituted into statements of conservation of mass or energy, such as the Fick principle (Calder, 1968; Lasiewski and Calder, 1971). These expressions include:

- (a) Capacity terms, approximately proportional to $M^{1.0}$
- (b) Frequencies, approximately proportional to $M^{-0.25}$
- (c) Flow rates, capacity \div time, $\propto M^{0.75}$
- (d) Periods or physiological time, $\propto M^{0.25}$
- (e) Fractional utilization, $\propto M^0$
- (f) Transfer coefficient, $\propto M^{0.5}$

Parallel evolution is seen when allometric expressions for physiological and anatomical variables of birds are compared with those for mammals. Despite the quite independent evolution, these slopes or exponents are undeniably similar. For example, Lasiewski and Calder (1971) compared respiratory variables of birds and mammals, and included an expression:

$$\text{total respiratory compliance (ml/cm H}_2\text{O)} = 5.83 M^{1.04}, n = 1 \quad (3)$$

The determination of a line's slope is difficult when there is only one point in the literature (that for the chicken, from Scheid and Piiper, 1969), so we borrowed the exponent for this function in mammals (Stahl, 1967). Many scientists are more comfortable when two or more points are used to establish a line, so with Crawford and Kampe's (1971) value for the pigeon, reanalysis provided a refined expression:

$$\text{total respiratory compliance (ml/cm H}_2\text{O)} = 5.86 M^{1.03}, n = 2 \quad (4)!$$

Allometric expressions, like the physiological and anatomical functions which they summarize, may be interrelated (Adolph, 1949; Stahl, 1967) and subjected to algebraic manipulations to solve for unknowns such as yet-undervived equations (Calder, 1968; Lasiewski and Calder, 1971). The necessity of keeping the physical dimensions clear in these relationships will be subsequently developed.

I shall use the standard symbols for respiration (Comroe, et al., 1950) and thermoregulation and conform to SI units as recommended by Gagge, et al. (1969). "The International System [S.I.] of Units is recommended by members of the General Conference on Weights and Measures for *all* scientific, technical, practical, and teaching purposes" (Mechtly, 1969; emphasis mine). This has particular utility when expressions of conversion efficiency, e.g., metabolic to mechanical in locomotion as Vance Tucker will be discussing (see, also, Barrow, 1973 for further strong argument for SI units). Hence this analysis will employ SI units. Conversions are: $\text{kcal} \times 4.184 \times 10^3 = \text{joules}$; $\text{cal} \times 4.184 = \text{joules}$; $\text{kcal} \cdot \text{hr}^{-1} \times 1.162 = \text{watts}$; $\text{kcal} \cdot \text{min}^{-1} \times 69.73 = \text{watts}$; $\text{kcal} \cdot \text{da}^{-1} \times 4.84 \times 10^{-2} = \text{watts}$; $1 \text{ watt} = 1 \text{ joule} \cdot \text{sec}^{-1}$ (Mechtly, 1969).

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METABOLISM AND ITS SUPPORT

The bird maintains itself in a thermodynamic steady-state, with a regulated body temperature (T_b), by extracting and converting energy from its environment. The metabolic conversions require oxygen. The relationships of metabolic support are summarized in Figure 4. Each

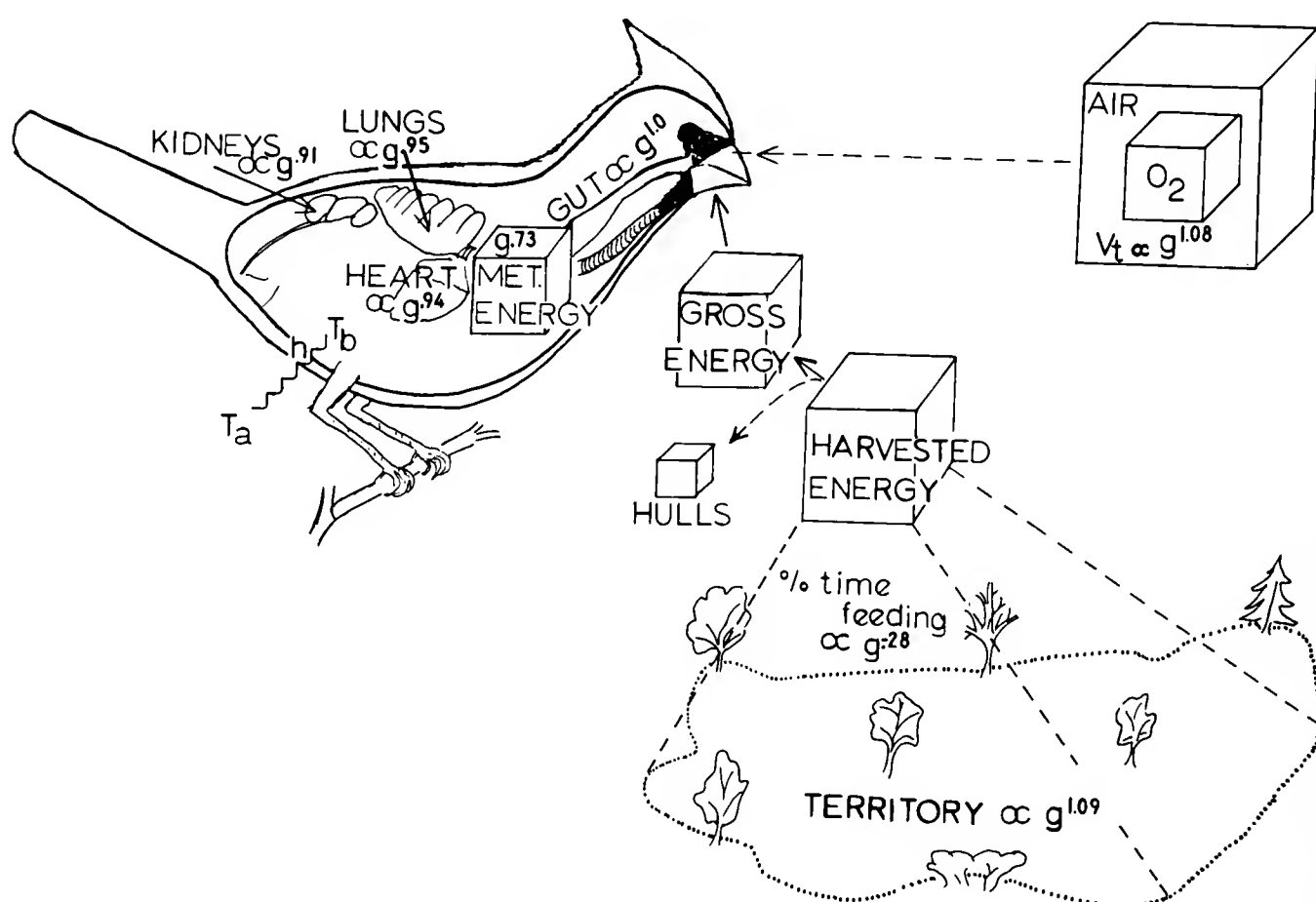


FIG. 4. Many aspects of avian energetics and metabolic support can be expressed allometrically. When the data have all been gathered, such a diagram could contain the essence of 100 pages of tables in the Handbook of Biological Data.

component has physical dimensions which should ultimately be measurable. Furthermore, once measured for a range of bird sizes, a power function can be derived. In going from one component to another there will be a fractional loss related to incomplete utilization and specific dynamic action.

Standard Metabolic Power (\dot{H}_{sm})

The standard thermoneutral metabolism (sometimes called basal metabolic rate) has been the most frequently measured variable in avian energetics, and therefore the one with the most data for allometric analysis. I will not repeat the history of refinements distinguishing birds and mammals, passerines and nonpasserines, and active (α) and rest (ρ) phases in the circadian cycle, which has been reviewed recently (Dawson and Hudson, 1970; Calder and King, 1974). The latest equations were provided by Aschoff and Pohl (1970). For purposes of this paper I will use their α equations, averaging together the expressions for their own data, and their recalculations from the

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data presented by Lasiewski and Dawson (1967). These are:

$$\text{Passerine: } \dot{H}_{sm} \text{ (watts} = 6.605 M^{0.72}; \text{ mWatts} = 46.63 m^{0.72} \quad (5)$$

$$\text{Nonpasserines: } \dot{H}_{sm} \text{ (watts} = 4.290 M^{0.73}; \text{ mWatts} = 28.67 m^{0.73} \quad (6)$$

$$(M = \text{mass in kg; } m = \text{mass in g})$$

Note that what has been studied as *energy metabolism* and loosely labelled as *energy*, is in fact *power*, or energy·time⁻¹, the dimensions of which are ml²t⁻³, where m = mass, l = linear dimensions, t = time. Metabolic power has been determined by indirect calorimetry, usually as oxygen consumption in volume consumed per time. This was multiplied by an energetic equivalent factor ("caloric equivalent"), generally assumed to be 4.8 cal. (ml O₂)⁻¹ for a respiratory quotient of 0.8. The energetic equivalent in SI units is simpler, 20.1 joules (ml O₂)⁻¹ (1 watt = 1 joule sec⁻¹).

The exponents in m^{0.72} and m^{0.73} are very similar to those of Kleiber (1961) for mammals, m^{0.75}. I will not review all of the attempts to explain this 3/4 exponent. Suffice it to say that whether heat loss or oxygen requirements were considered, it could only be concluded that metabolic rate was a compromise between linear-scaling and a body surface (m^{0.67}) consideration. However, an excellent analysis by McMahon (1973) approaches scaling from the viewpoint that elastic stability and flexure, not resistance to direct compression forces, set limits on body size and the dimensions of body-supporting members. McMahon predicts that metabolic power output should be proportional to m^{0.75}.

Oxygen Supply (\dot{V}_{O_2})

In the long run, oxygen uptake must balance the oxygen consumption of metabolism (\dot{V}_{O_2}), although a bird may incur a short-term oxygen debt, in a spurt of intense activity or in diving. According to the First Law of Thermodynamics, matter and energy cannot be created or destroyed. Thus we should be able to account for the flow of matter in a supply system. In a steady-state, the rate of flow at any level in a continuous system is the same when all the branches are measured:

$$\begin{aligned} \dot{V}_{O_2} \text{ respiratory uptake} &= \dot{V}_{O_2} \text{ transported in blood} = \dot{V}_{O_2} \text{ consumed} \\ &= \frac{\text{metabolic power}}{k} \end{aligned} \quad (7)$$

where k = 20.1 j(ml O₂)⁻¹. Oxygen is delivered to avian tissues by two cyclical, mechanical pumps in turn, the thorax-lung-air sac pump and the heart. The oxygen is incompletely removed from each preceding stage. Consequently, the delivery is quantitatively characterized as the product of three variables:

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$$\text{pumping rate} \times \text{pump stroke} \times \text{fractional removal} = \text{rate of transport} \quad (8)$$

or

$$\text{frequency (f)} \times \text{capacity (V)} \times \text{concentration change } (\Delta\%) = \dot{V}_{O_2} \propto \dot{H}_m \quad (8a)$$

For each variable, we can substitute an allometric expression just as easily as an individual determination. If all of the allometric expressions accurately describe their variables, the product of the left side of the equation should equal the \dot{H}_m expression obtained independently.

What has this manipulation to do with avian energetics? Birds have the reproductive capacity to exceed the energy (food) supply and their ability to reproduce is contingent upon obtaining adequate food. Part of the energy intake must be used to pay the costs of foraging, as well as pumping air and blood to supply energy and oxygen to the tissues. These costs should be minimized for optimal performance and energetic economy. If there is a selection for increase or decrease in body size, the total metabolic requirements change nonlinearly with respect to body mass, and all of the supply variables must be altered appropriately to meet these demands while attaining maximum efficiency (in terms such as the ratios of energy available for work, reproduction and growth to total energy intake, or work output to energy input).

Let us consider the allometry of the supply functions of respiration, circulation, feeding, and digestion and then we can return to the subject of the optimization through natural selection.

Respiration.—The total oxygen consumption is the product of respiratory rate (f_r), tidal volume (V_T), and concentration difference between inspired ($F_{I_{O_2}}$) and expired air ($F_{E_{O_2}}$). Lasiewski and Calder (1971) assembled the available information for resting non-passerine birds into the appropriate exponential functions:

$$f_r \times V_T \times (F_{I_{O_2}} - F_{E_{O_2}}) = \dot{V}_{O_2} \quad (8b)$$

$$17.2 M^{-0.31} \times 13.2 M^{1.08} \times ? M^{\text{exp?}} = 11.3 M^{0.72}$$

Solving for $(F_{I_{O_2}} - F_{E_{O_2}})$, they predicted $0.05 M^{-0.05}$, which suggested that resting birds reduce the oxygen content of air respired from 21% to 16%, and that this is probably independent of body size (small exponent), as it is in mammals (Stahl, 1967). This is also consistent with the similarities in tissue gas tensions and percent respiratory dead-space in mammals (Tenney and Bartlett, 1967; Tenney and Morrison, 1967) and tracheal dead space in birds ($3.72 M^{1.09}$; Hinds and Calder, 1971).

The total volume should be proportional to the size of the respiratory system. If the tidal volume exponent (1.08) can be accepted as

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approximately linear, the exponents for lung mass $M^{0.95}$, lung volume $M^{0.94}$, and total respiratory system volume $M^{0.91}$ can also be regarded as linear (Lasiewski and Calder, 1971).

Circulation.—It should be possible to account for \dot{V}_{O_2} in the circulation using equation (8a), since this function stands between respiration and tissue oxygen consumption. However, too many unknowns remain in the circulation equation. The heart rate (f_h) has been analyzed for birds, without distinguishing between passerines and other birds (Calder, 1968; Lasiewski and Calder, 1971):

$$f_h, \text{ min}^{-1} = 155.8 M^{-0.23} \text{ or } 763 m^{-0.23} \quad (9)$$

Stroke volume and arterial-venous O_2 difference have not been measured over any size range in birds. Such information should be available for baseline considerations when, for example, f_h , easily telemetered, is to be used as an index of metabolic power (Owen, 1969).

Heart weight has been suggested as an index of stroke volume. Delbert Kilgore (pers. comm.) informs me that he and Knut Schmidt-Nielsen have obtained heart weights of rheas and, with published values find that:

$$m_{\text{heart}} = 8.56 M^{0.94} \quad (10)$$

Using this as an index of stroke volume, an index of cardiac output rate (rate \times stroke volume) can be obtained, as suggested by Lasiewski and Calder (1971):

$$155.8 M^{-0.23} \times 8.56 M^{0.94} = 1334 M^{0.71} \quad (11)$$

which can be compared with equations for mammals given by Stahl (1967):

$$241 M^{-0.25} \times 5.8 M^{0.98} = 1398 M^{0.73} \quad (11a)$$

Stahl gives an equation for cardiac output in mammals:

$$\text{cardiac output (ml} \cdot \text{min}^{-1}) = 187 M^{0.81} \quad (11b)$$

so the "index" should be corrected by a factor of $0.13 M^{0.08}$, at least in the case of mammals.

From this it is seen that on an equal body size basis, the avian heart is larger and beats slower. The product suggests that cardiac output at rest is very similar for birds and mammals. What about the energetic demands of flight? The heart rate during flight of eleven species of birds (Table 3 in Berger, et al., 1970; Aulie, 1971) is 2.61 times the resting rate (highest/lowest; range 1.82-3.77). Mammals elevate heart rate in exercise by about the same factor, 2.6 (bat, *Eptesicus fuscus*: 2.14, Studier and Howell, 1969; dog: 3.0, Donald and Ferguson, 1966; man: 2.67, Selkurt, et al., 1966). Thus the energetic demands of flight in birds cannot call upon heart rates as high as mammals for the avian heart starts slower and expands by a similar multiple. Consequently, the avian heart rate in exercise is still about

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65% of the mammalian rate, if animals of similar weight are considered.

Fuel Supply

I have dealt with the oxygen supply first, for two reasons. First, oxygen consumption is what is usually measured as "metabolism." Second, it is easier to obtain precise measurements, in controlled conditions, of how much oxygen a bird consumes, f , V , and $\Delta\%$, than it is to measure the analogous variables in a feeding equation. Consequently, the allometrician has at his disposal fewer data of a more variable nature, if he is considering feeding, digestion, or ecological aspects of energetics. The following is submitted as speculation only, with the hope of stimulating the collection of sufficient data to support or refute it.

Difficulties notwithstanding, Adolph (1949), McNab (1963), Helms (1968), Schoener (1968), Kendeigh (1969, 1970), Pulliam and Enders (1971), Willson (1971), and Fretwell (1972) have considered digestion and feeding in regard to effects of body size. Analysis at this point can perhaps tell us not only the utility of the information we have collected so far, but what should be collected in the future.

Information on food intake in nature, or the energetic cost of free life in birds, is very limited with respect to size and phylogenetic ranges. Upon the limited data are superimposed the complexities of temperature, photoperiod, and migratory and reproductive status, which vary the total energetic demands.

Somewhere between metabolic levels for birds under standard and wild conditions is the existence energy (\dot{H}_{ex}), which is calculated from food intake and represents the sum of standard thermoneutral metabolism, thermoregulatory increments, specific dynamic action (heat increments of feeding), and physical activity within the confines of the cage dimensions.

Kendeigh (1969, 1970) has summarized the existence metabolism as follows (converted to SI units) (see Figure 7).

Passerines, 30°C:

$$\begin{aligned}\dot{H}_{ex}, \text{ watts} &= 5.553 M^{0.62}; mW = 76.14 m^{0.62}, n = 15; \\ \bar{M} &= 0.024\end{aligned}\tag{12}$$

Nonpasserines, 30°C:

$$\begin{aligned}\dot{H}_{ex}, \text{ watts} &= 4.800 M^{0.75}; mW = 26.17 m^{0.75}, n = 9; \\ \bar{M} &= 1.264\end{aligned}\tag{13}$$

All birds, 0°C:

$$\begin{aligned}\dot{H}_{ex}, \text{ watts} &= 8.171 M^{0.53}; mW = 210.03 m^{0.53}, n = 24, \\ \bar{M} &= 0.470\end{aligned}\tag{14}$$

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The first two may be compared with predictions for \dot{H}_{sm} , using the mean body masses for Kendeigh's equations above in equations (5) and (6) (see Table 1). From this it appears that existence metabolism is 12 to 40% higher than standard metabolism, but the biological significance of \dot{H}_{ex} does not lie in relation to \dot{H}_{sm} but in relation to metabolism in the wild, allometric analysis of which awaits adequate data.

Feeding and Digestion.—The digestive system and processes, as well as the feeding patterns of birds, must be scaled to fulfill the metabolic requirements of any body size. Is it possible that the processes of energy-delivery could be analyzed by analogy to the delivery of oxygen? What variables, described allometrically, would be suitable multipliers in the mass-conservation equation (8a)?

There are several variables involved in the energy supply, which have been or could be, quantified and then analyzed allometrically. These include frequency and duration of feeding, time of passage of a bolus through the gut, gut weight or capacity, volume of crop, weight of fat depots, volume or weight of food captured or ingested, fractional harvesting, and fractional absorption from the gut (or utilization coefficient).

The weight of the digestive tract should be an index of the capacity of the system. A factor with the units of cm^3g^{-1} would convert gut weight to capacity of the digestive system. The utilization factor ($\Delta\%$) would describe the fractional filling and absorption of gut capacity per feeding. To obtain a consumption rate (\dot{V}), we must multiply $V \cdot \Delta\%$ by frequency of feeding (f). If there were sufficient data for allometric expression for each of these factors, the product (consumption rate \dot{V}) should have a slope parallel to that for the appropriate expression of metabolic rate or power input.

Brody (1945) derived the following relationship for birds:

$$\text{gut mass} = 0.0997 m^{0.985} \quad (15)$$

and the data tabulated by Quiring (1950) yield a nearly identical expression:

$$\text{gut mass} = 0.096 m^{1.003} \quad (15a)$$

In all likelihood, there is a direct correlation between gut mass and gut volume.

Of course, great differences exist in the morphology of the digestive system, which can be correlated with food habits (see Van Tyne and Berger, 1959; Ziswiler and Farner, 1972). The grit capacity of the gizzard is approximated as a function of $m^{1.1}$ (goose, duck, turkey; see Welty, 1962, p. 91).

These approaches to the capacity variable are not entirely satisfactory, but the frequency term is even more difficult to define. Gibb (1954) observed that the proportion of time spent in feeding was inversely related to body size in a series of tits (*Parus* spp. and *Aegithalos caudatus*), the Brown Creeper (*Certhia familiaris*), and the Goldcrest

TABLE 1
A Comparison of Existence Metabolism and Standard Metabolism.

Birds	Mean mass (kg)	Predicted		
		\dot{H}_{ex}^1 (watts)	\dot{H}_{sm} (watts)	$\dot{H}_{ex}/\dot{H}_{sm}$
Passerines, 30° C	0.024	0.550	0.450 ²	1.22
Nonpasserines, 30° C	1.264	5.722	5.090 ²	1.12
All Birds, 0° C	0.470	5.476	3.905 ³	1.40
			Mean	1.25

¹ From equations (12), (13), and (14) in text; ² From equations (5) and (6) in text; ³ Using equation (5) of Lasiewski, et. al., 1967, for a regression from $T_b = 40^\circ\text{C}$.

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(*Regulus regulus*). The size range of 5 to 18 g is small, but monthly values collected in a standard procedure from November through March yield power functions averaging $m^{-0.28}$, similar to standard metabolic rate per gram, and to respiratory and heart frequency, and each is significant at the .01 or .001 levels ($m^{-0.21}$, $m^{-0.16}$, $m^{-0.27}$, $m^{-0.37}$, $m^{-0.41}$). Percent of time is, however, a dimensionless factor:

$$\% \text{ of time} = \frac{\text{number of trips} \times \text{mean trip duration}}{\text{daylength}} = \frac{\text{hr.}}{\text{hr.}} \quad (16)$$

Since the frequency of feeding is the number of trips per day, then:

$$f = \frac{\% \text{ of time}}{\text{mean trip duration}} = \text{hr}^{-1} \quad (17)$$

So if "mean trip duration" is not size-dependent, percent of time feeding should be a function of $\sim m^{-0.25}$.

Willson (1971) has studied selection of commercial seeds by 8 species of finches. From data on preference and/or husking and eating times, she calculated the potential caloric yield per minute of feeding. She did not list body weights, so I have borrowed values from Weatherbee (1934, for Fox Sparrow), Stewart (1937), and Nice (1938) as approximations and obtained a regression:

$$\text{cal/min} = 11.81 m^{1.02}; r = 0.90, s_m = 0.216, \log s_b = 0.293 \quad (18)$$

or

$$\text{joules/min} = 49.4 m^{1.02} \quad (18a)$$

If insectivorous passerines and seed-eating passerines have parallel relationships for rate of energy intake (eqn. 18a) or for percent time spent feeding ($m^{-0.28}$; eqn. 17) the products should be:

$$\text{joules/min. feeding} \times \text{joules/min. feeding/day} = \text{joules/day} \quad (19)$$

or

$$m^{1.02} \times m^{-0.28} = m^{0.74} \quad (19a)$$

which is certainly similar, exponentially, to the metabolic rate-body mass relationship (eqn. 5). H. R. Pulliam (pers. comm.) points out that the commercial seeds provided by Willson were all larger than the normal food seeds of the smaller species. Obviously, the variables in equation 19a should be reanalyzed, allometrically, when more appropriate data are available.

If there is merit to an allometric consideration of feeding and digestion, particular care must be given to the dimensions of the variables involved. Fretwell (1972) has analyzed metabolic requirements and the capacities of sparrows for meeting these requirements. From this he proposed a theory of body size for sparrows. Three variables in his model were metabolic energy or "metabolic needs" (ME), digestive energy or metabolic capacity (DE), and captured energy or ecologic

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capacity (CE). A minimum metabolic energy requirement can be determined for a given body size. A successful sparrow must be able to capture, process, and absorb enough energy-yielding substrate to meet the metabolic requirements. If ME, DE, and CE have different exponential powers of body mass, their intersections would define minimum, optimum, and maximum body size for birds of a given type such as sparrows.

Fretwell's model is stimulating, having brought the energy supply process into an allometric perspective, but the particular energetic variables used were, unfortunately, dimensionally inconsistent. Metabolic rate (energy divided by time) is *power* (ml^2t^{-3}), with units of watts or mWatts (previously expressed as $\text{kcal}/\text{bird}\cdot\text{day}$). DE is related to a weight which is proportional to volume or capacity of the digestive tract. For a given diet this capacity can be multiplied by a mean energetic equivalent ($\text{joules}/\text{cm}^3$ or j/g), to give a total of *ingested energy*, and by a fraction for absorption to give *digested energy* (ml^2t^{-2}). Note that this is lacking a frequency term (t^{-1}) which would be necessary to relate DE to ME. Because of the differences in dimensions of these variables as defined, their intersections on a graph cannot have any significance with regard to a minimum body size for a type of sparrow.

Territory and Home Range.—Birds depend upon their environment for food. One of the suggested functions of territoriality is to achieve spacing for optimum exploitation of food resources (Von Haartman, 1971). Areas not defended as territories, but utilized for feeding are included in the home range of an animal. McNab (1963) analyzed the home ranges of mammals allometrically and concluded that the area of the home range had an exponential relationship to body mass similar to that characterizing the standard metabolism (0.63 vs. 0.75). However, Schoener (1968) found higher exponents for territory (1.09 for all birds, 1.31 for carnivorous birds) and home range (1.16 for all birds, 1.39 for carnivorous birds). For lizards the home range is proportional to $m^{0.95}$ (Turner *et al.* 1969).

Why do reptiles and birds have higher exponents than mammals? Buskirk (unpub.) has re-analyzed home ranges of mammals with additional data. In addition, he has divided mammals into primary and secondary consumers instead of "croppers" and "hunters" used by McNab (1963). He found:

$$\text{Primary consumer home range, ha.} = 4.74 M^{1.024}, n = 32, r = 0.934 \quad (20)$$

$$\text{Secondary consumer home range, ha.} = 66.8 M^{1.223}, n = 8, r = 0.956 \quad (21)$$

Schoener (1968) derived a higher ($M^{1.41}$) proportional relationship for predatory mammals and noted that this exponent was similar to that for predatory birds. Without trying to dabble in the theoretical ecology

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of feeding strategy, about which I am quite ignorant, I will merely observe that the home range or territory category is a capacity term, (biomass or energy yield per unit surface) which could be expressed in the dimensions of energy, and that multiplication by a frequency term would be necessary if one wished to relate this to metabolic power ($M^{0.72}$ to $M^{0.73}$) or to rate of food consumption:

$$g \text{ food/day} = 0.53 m^{0.63}, n = 19, s_b = 0.09, s_m = 0.03 \quad (22)$$

from the tabulated data of Nice (1938). The exponent of 0.63 is less than that expected from consideration of thermoneutral metabolism, but is intermediate between the thermoneutral and 0°C exponents. Incidentally, it is identical to McMahon's (1973) exponent for surface area as a function of body weight of a stretched cylinder.

Optimization of the Supply Functions

How might the variables in the equation:

$$f \times V \times \Delta\% = \dot{H}_m \quad (8a)$$

be modified to meet new requirements most efficiently, when the whole bird is scaled up or down for the exploitation of some ecological advantage? The vegetative organs or supply systems (lungs, heart, blood, kidneys, gut) must be transported in flight. The weight involved would, logically, be minimized in both large and small birds, perhaps to a size-independent fraction of body mass, i.e., organ mass = $M^{1.0}$. Size of organ can be used as an index of its stroke volume when pumping (Stahl, 1967; Lasiewski and Calder, 1971), and this suggests that $V \propto M^{1.0}$ in equation (8a).

It would be wasteful to go to the trouble of pumping, and then only extract an insignificant fraction of the intake. On the other hand extraction of oxygen is limited by the passive process of diffusion, so that complete extraction is also not possible. When it comes to the analog in feeding, extraction of prey (capture) is limited by the concealing vegetation and topography.

Hence, in any supply process, utilization below 100% extraction is probable, even in activity, and would be even less during rest. Whatever variation might exist, distributed over a body mass range of 10^5 (hummingbird to ostrich), would leave little opportunity for a slope differing significantly from zero on the log-log plot. Consequently, we might expect $\Delta\%$ in equation (8a) to be proportional to M^0 .

This leaves f as the variable which could balance the equation, exponentially. A. V. Hill (1950) pointed out that "similar animals should carry out similar movements not in the same time, but in times directly proportional to their linear dimensions." Assuming that the muscles of a small and a large bird have the same density and intrinsic strength (maximum force per unit cross-sectional area), they should undergo the same inertial stress (force per unit area) at any point. Force per unit area has the dimensions of $ml^{-1}t^{-2}$, so

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$$m_1 l_1^{-1} t_1^{-2} = m_2 l_2^{-1} t_2^{-2} \quad (23)$$

where 1 = small bird and 2 = large bird. Dividing through by the same density (ml^{-3}):

$$l_1^2 t_1^{-2} = l_2^2 t_2^{-2} \quad (23a)$$

$$\therefore l_1 : t_1 = l_2 : t_2 \quad (23b)$$

Thus Hill concluded that the contraction or movement times are proportional to linear dimensions or $M^{0.33}$. Frequency is the reciprocal of time period, so that:

$$t^{-1} = f \propto M^{-0.33} \quad (23c)$$

This exponent approaches those for f_r , f_h , and f_g of mammals ($M^{-0.26}$, $M^{-0.25}$, $M^{-0.31}$) for f_r of nonpasserine birds ($M^{-0.31}$) (Adolph, 1949; Stahl, 1967; Calder, 1968). Also starting from the reasoning of Hill's (1950) paper, but bringing in theory for bending beams, McMahon (1973) concluded that frequency *should* be a function of $M^{-0.25}$.

McMahon's line of reasoning may be summarized as follows. The critical length for buckling of a column is a function of its diameter (d) to the $2/3$ power:

$$l \propto d^{2/3} \quad (24)$$

While weight (kg) is:

$$M \propto l \cdot d^2 \quad (25)$$

Substituting from (24):

$$M \propto d^{2/3} \cdot d^2 = d^{8/3} \quad (26)$$

So:

$$d \propto M^{3/8} \quad (27)$$

The maximum power output of muscles is proportional to their cross-sectional area or d^2 . Thus metabolic power output (\dot{H}_m) is:

$$\dot{H}_m \propto d^2 = (M^{3/8})^2 = M^{3/4} \quad (28)$$

Hemmingsen 1960 and Hart and Berger (1972) have shown that the ratio of exertion to resting metabolic power is independent of size so that resting metabolic level and probably alveolar ventilation are also related to functions of $M^{3/4}$. Lung volumes and tidal volumes are essentially linearly proportional to size ($M^{1.0}$), so respiratory frequency should be a function of $M^{3/4} \div M^{1.0} = M^{-1/4}$, as are a number of frequency variables, e.g., heart rate, mammalian gut pulse, etc. (see above; also Adolph, 1949; Stahl, 1963; McMahon, 1973).

Tracheal Design.—Energetic supply processes are less than 100% profitable; that is, part of the intake is consumed in the process. The

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bird must expend energy to feed and obtain more energy. To supply oxygen to the tissues, oxygen must be consumed by the respiratory pump and the circulatory pump. An obvious advantage would exist for minimizing the cost of pumping.

As a bird breathes to obtain oxygen, oxygen must be consumed in the work of breathing. This work must overcome elastic reactance, inertial reactance, and functional resistance (Hull and Long, 1961). As a class, birds have longer tracheae, than do mammals, when comparison is made between animals of the same body mass. Tracheal lengths (cm.) of mammals were $6.2 M^{0.40}$, whereas birds have tracheae of length $16.77 M^{0.39}$ (Tenney and Bartlett, 1967; S. M. Tenney, pers. comm.; Hinds and Calder, 1971). The resistance to flow is directly proportional to length, so the bird trachea offers 2.7 times as much resistance as does the mammals. At the same time, the birds tracheal diameter is 1.29 times that of the mammal ($0.53 M^{0.35}$ and $0.41 M^{0.39}$, respectively). If the airflow in the trachea is laminar, resistance is inversely proportional to the fourth power of the radius according to Poiseuille's law. Thus, the larger cross-section of the avian trachea reduces resistance by a factor of 1.29^4 or 2.77, very similar to, but counterbalancing the increase in resistance caused by the larger windpipe.

However, increases of diameter and length both increase the dead-space or volume of air which must be pumped without taking place in the gas exchange. The allometric relationships indicate that this increase in dead space would equal the product of 2.7 times 1.29^2 , or 4.5 times as much dead space. The physiological significance of this dead-space lies in how often it is ventilated (dead-space ventilation, $\text{cm}^3\text{min}^{-1}$) or in what proportion of the total ventilation is of no value for gas exchange. By exchanging larger tidal volumes less frequently than mammals (avian $f = 0.34$ to 0.42 times mammalian f), the birds significantly reduce the effect of larger dead-space. These factors have been drawn together in a speculative scheme for the allometric evolution of avian respiration (Fig. 5). If this scheme is reinforced by further examination, a good example of optimization in a supply function will be established.

Physiological Time

Hill (1950) offered another interesting concept concerning physiological time: "The mouse may live at a metabolic rate 100 times that of the elephant, the hummingbird at 100 times the rate of the stork; if so, on their own scale of time the day and the season are 100 times as long to the small animal as to the large. This is found to affect their economy, as ours would be affected if nightfall and sunrise occurred every three months, if winter returned every 100 years."

Since frequencies of heartbeat and respiration are functions of $M^{-1/4}$, the duration of one heart or respiratory cycle is the reciprocal, $M^{1/4}$. A parallel function is seen in the time for a bird to metabolize an amount

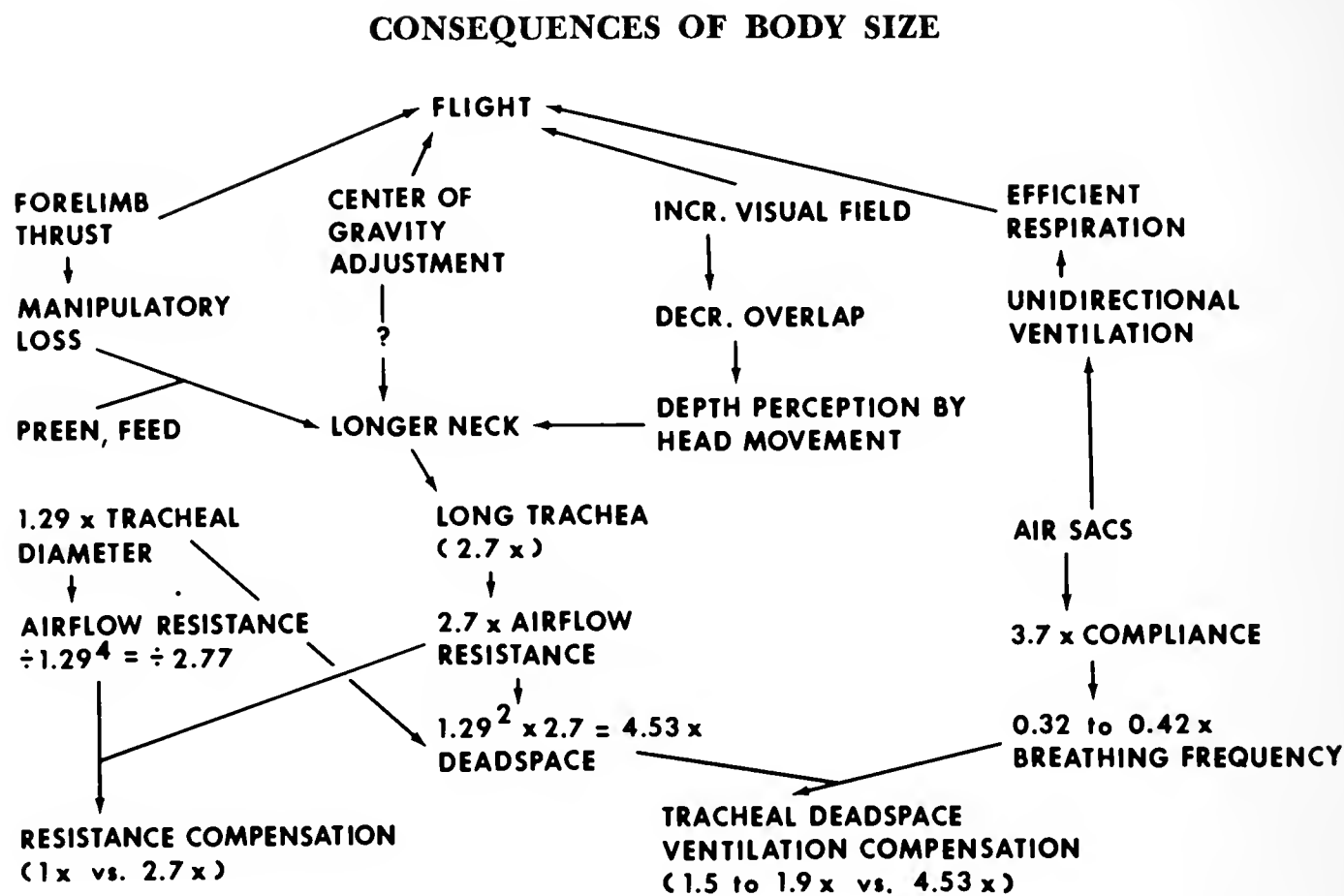


FIG. 5. A speculative scheme for the interaction of respiratory morphology and mechanics with avian evolution for flight. Values for multiples (e.g. "1.29 ×") compare the coefficients in avian and mammalian power functions for particular variables. Tracheal and resistance factors were derived from measurements by Tenney and Bartlett (1967, mammals) and Hinds and Calder (1971, birds). Compliance factor from Lasiewski and Calder (1971) and data of Crawford and Kampe (1971). Breathing frequency factor from Calder (1968) and Lasiewski and Calder (1971). (Reprinted from *Evolution* with permission.)

of food equivalent to body weight (M^1), at a metabolic rate $\propto M^{-3/4}$:

$$M^1/M^{3/4} = M^{1/4} \quad (29)$$

The longest period of physiological time is the lifespan. Record lifespans (t_{ls}) of birds have been related to body mass as follows (S. Lindstedt, pers. comm.):

$$\text{Captive birds: } t_{ls} = 7.63 m^{0.19} \quad (30a)$$

$$\text{Natural maxima for wild birds: } t = 4.44 m^{0.20} \quad (30b)$$

$$\text{Wild passerines: } t = 3.57 m^{0.23} \quad (30c)$$

$$\text{Wild non-passerines: } t = 4.79 m^{0.18} \quad (30d)$$

$$\text{Mammals (Gunther and Guerra, 1955): } t = 7.52 m^{0.29} \quad (30e)$$

These exponents for birds are slightly less than those for shorter physiological time scales, e.g., equation (15). Note that the larger the bird the longer the lifespan. Thus, in the relatively limited history of bird-banding, there have been more lifespans elapsed for small than large birds, so that after another decade or two of banding, the regression slopes or exponents for lifespans of birds and mammals may turn out to be more similar!

Regardless of the exact exponent (the ultimate truth) it is obvious

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that physiological time is not independent of body size, but may increase as the 4th root of body mass, for time scales of heart cycle or breath duration to lifespan. Birds must live in conformity with the earth's time and cycles of light and darkness. As Aschoff (1967) pointed out, "There are niches in time as well as in space. The dichotomy of the living world into diurnal and nocturnal species can be considered as an example of such a temporal specialization . . . a temporal niche offers a programme which can be incorporated into the organism itself. In developing a self-sustained rhythm of approximately the same frequency as that of the environment, the organism, when entrained, anticipates in its own organization, the respective states it needs in order to react properly to the environmental conditions which will ensue—it is prepared in advance."

As I indicated above, Aschoff and Pohl (1970a,b) have shown that the standard metabolic rate is lower during the rest (ρ) phase of the daily cycle than during the active (α) phase (night and day, respectively, for most birds). However, body size appears to have parallel effects for ρ and α phases (similar exponents or slopes of log-log functions). Aschoff (1967) has discussed the influences of season and latitude upon α -durations and phase-angle differences, but there does not seem to be any obvious body size influence in this. From equation (29) we might expect that shortening daylength would create a problem, the severity of which would be inversely related to body size. That this does not appear to be the case suggests that either the reality of the earth's rotation has caused the small birds to rise above the constraints of allometry, or we have overemphasized the significance of body size, that in this case, body size is not limiting. I will return to this, to reconsider Bergmann's Rule.

THERMOREGULATION

SMR at Thermoneutrality and at 0°C

The allometry of: $(f \propto m^{-1/4}) \times (V \propto m^1) \times (\% \propto m^0) \times (\text{joule cm}^{-3}\text{O}_2 = \dot{H}_m)$ (8a) was (almost) neat for respiration and circulation, but it got rather messy when we attempted to plug in field observations for feeding and territory. The allometric accountability is once again respectable when thermoregulation is analyzed, doubtlessly because the thermoregulation was studied in the laboratory where the variables can be reduced and controlled.

When a bird is maintaining a body temperature (T_b) constant and different from the mean environmental temperature (T_a) the rate of heat production (\dot{H}_m) must equal the rate of evaporative and non-evaporative or "dry" heat loss (\dot{H}_{dl}). The last term is the simplified sum of heat loss by radiation (\dot{H}_r), convection (\dot{H}_c), and conduction (\dot{H}_k). In the uniform environment of a metabolic chamber, the "dry" heat loss has been approximated by the model of Scholander, et al. (1950) which has stimulated over two decades of comparative physi-

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ology and remains a useful basis for analysis after its limitations are understood (see Tracy, 1972). It states that heat loss is proportional to the temperature difference between the bird's body and its environment (see Fig. 6):

$$\dot{H}_m - \dot{H}_e = \dot{H}_{dl} = h(T_b - T_a) \quad (31)$$

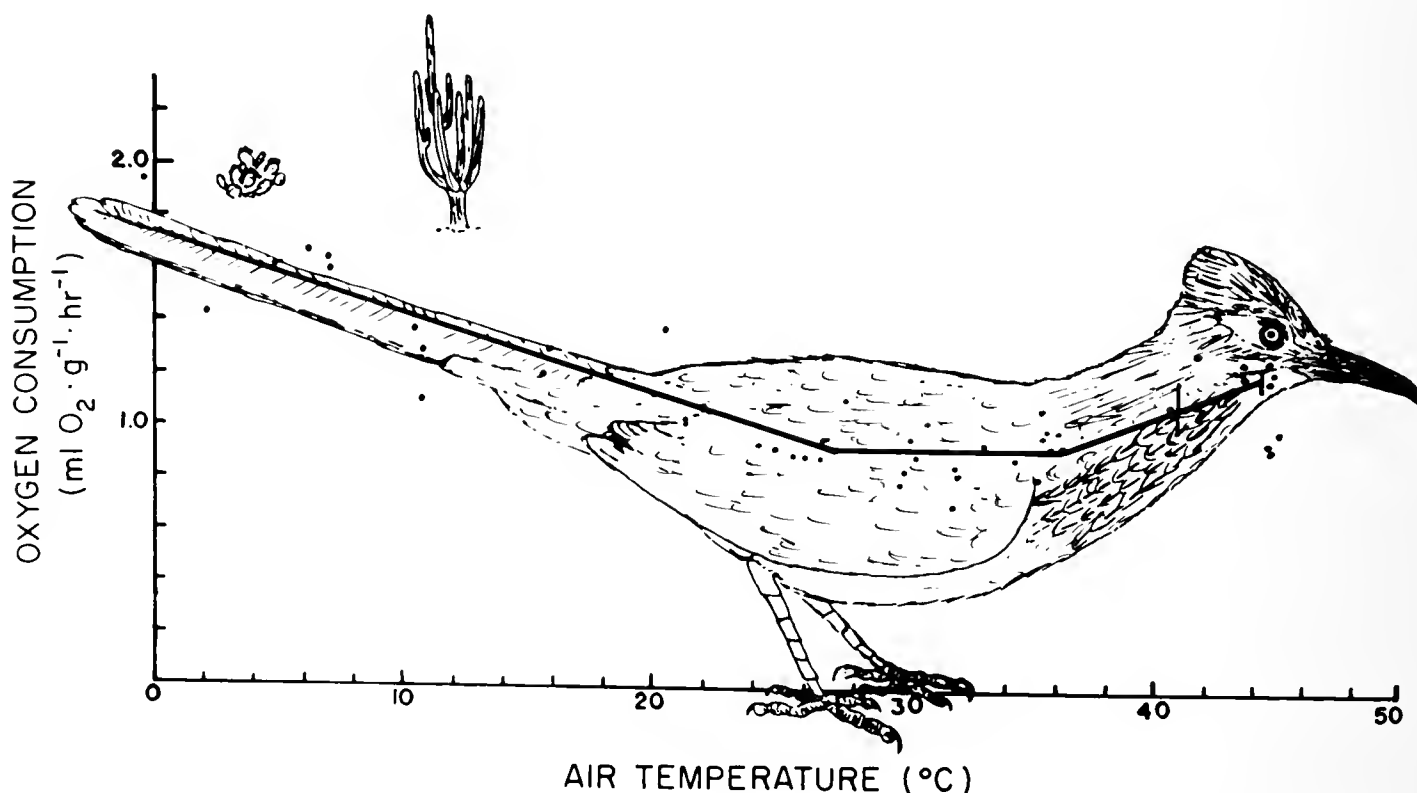


FIG. 6. A typical plot relating the oxygen consumption of a bird to the temperature in a respiration chamber. The similarity in the shape of the metabolic curve to the shape of the Roadrunner may support the "doctrine of signatures"; on the other hand it may reflect parental influence, my father being an astronomer. Data from Calder and Schmidt-Nielsen (1967) show a thermoneutral zone (27-36°C) below which metabolism must increase to balance heat loss and above which the metabolic effort of panting plus the Q_{10} effect of hyperthermia are seen.

where h = heat transfer coefficient, with units of mWatts $(^{\circ}\text{C})^{-1}$. This has often been referred to as "thermal conductance," but as data have accumulated and avian biologists have become more aware of physical principles, the more inclusive term has been revived from Burton's (1934) usage by Gagge, et al. (1969). Herreid and Kessel (1967) and Lasiewski, et al. (1967) obtained very similar allometric expressions for the heat transfer coefficient when converted to common units. The data from both, with additional values published subsequently, have been used to derive separate expressions for passerine and other birds (Calder and King, 1974). Expressions as units of cal $(\text{hr } ^{\circ}\text{C})^{-1}$ per g body mass are improper, according to Kleiber (1972). Hence I will convert the equations of Calder and King to mWatts per bird to conform to SI units and Kleiber's exhortations:

$$\text{Passerines: } h, \text{ mWatts } ^{\circ}\text{C}^{-1} = 5.29 m^{0.46} \quad (32)$$

$$\text{Nonpasserines: } h, \text{ mWatts } ^{\circ}\text{C}^{-1} = 4.72 m^{0.46} \quad (33)$$

These lines are not significantly different, but are left distinct for use

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with variables which have statistically significant differences in equations (5) and (6). A comparable expression for mammals is very similar $5.30 \text{ m}^{0.50}$ (units converted from Hart, 1971). Returning to equation (31), important points must be made. Heat loss occurs through the body surface, so that the heat transfer coefficient can also be expressed quite appropriately as $\text{mWcm}^{-2} \text{ }^{\circ}\text{C}^{-1}$, using the Meeh approximation:

$$\text{Body surface (cm}^2\text{)} = S = 10 \text{ m}^{2/3} \quad (34)$$

the reliability of which has been carefully verified for birds by Drent and Stonehouse (1971; their Fig. 7). Note however, that for animals $\text{m}^{0.63}$ is preferable on theoretical grounds according to McMahon, 1973). Thus h can be expressed per unit surface as:

$$\text{Passerines: } h, \text{ mWcm}^{-2} \text{ }^{\circ}\text{C}^{-1} = 0.529 \text{ m}^{-0.21} \quad (35)$$

$$\text{Nonpasserines: } h, \text{ mWcm}^{-2} \text{ }^{\circ}\text{C}^{-1} = 0.472 \text{ m}^{-0.21} \quad (36)$$

Air velocity changes the value of h significantly (Tracy, 1972) but the rates of air flow normally imposed within the metabolic chamber are sufficiently low that h would not be influenced.

The smaller the bird, the more rapidly its body temperature changes in heat stress, physical activity, and psychic excitement. Once this lability is taken into account, there does not appear to be a body size effect upon the mean body temperature, i.e., $T_b \propto \text{m}^0$ (Calder and King, 1974). With this, we can substitute allometric expressions (5), (6), (32), and (33) in equation (31):

Passerines, thermoneutrality:

$$\dot{H}_m = 46.63 \text{ m}^{0.72} = 5.29 \text{ m}^{0.46}(40^{\circ} - T_{lc}) \quad (31a)$$

Nonpasserines, thermoneutrality:

$$\dot{H}_m = 28.67 \text{ m}^{0.73} = 4.72 \text{ m}^{0.46}(40^{\circ} - T_{lc}) \quad (31b)$$

Solving for $(40^{\circ} - T_{lc})$, we see that the lower critical temperature (T_{lc}) is proportional to $\text{M}^{0.27}$, as shown for mammals by Morrison (1960), rediscovered by Kleiber (1972a), and extended to birds by Dawson and Hudson (1970) and Calder and King (1974).

When equation (31) is considered for lower temperatures, below thermoneutrality, the exponent for metabolism decreases, because \dot{H}_m includes the basal level plus the increment for offsetting the effects of a larger temperature differential, the latter being a larger displacement from thermoneutrality, the smaller the bird. This insight comes from Kendeigh's (1969) very useful expressions of standard metabolism at 0°C . (We must constantly remind ourselves that what is convenient as a baseline in the lab may seldom be encountered by a free bird, so that if used alone, thermoneutral standard metabolism's $3/4$ exponent should be taken with caution in erecting grand theories).

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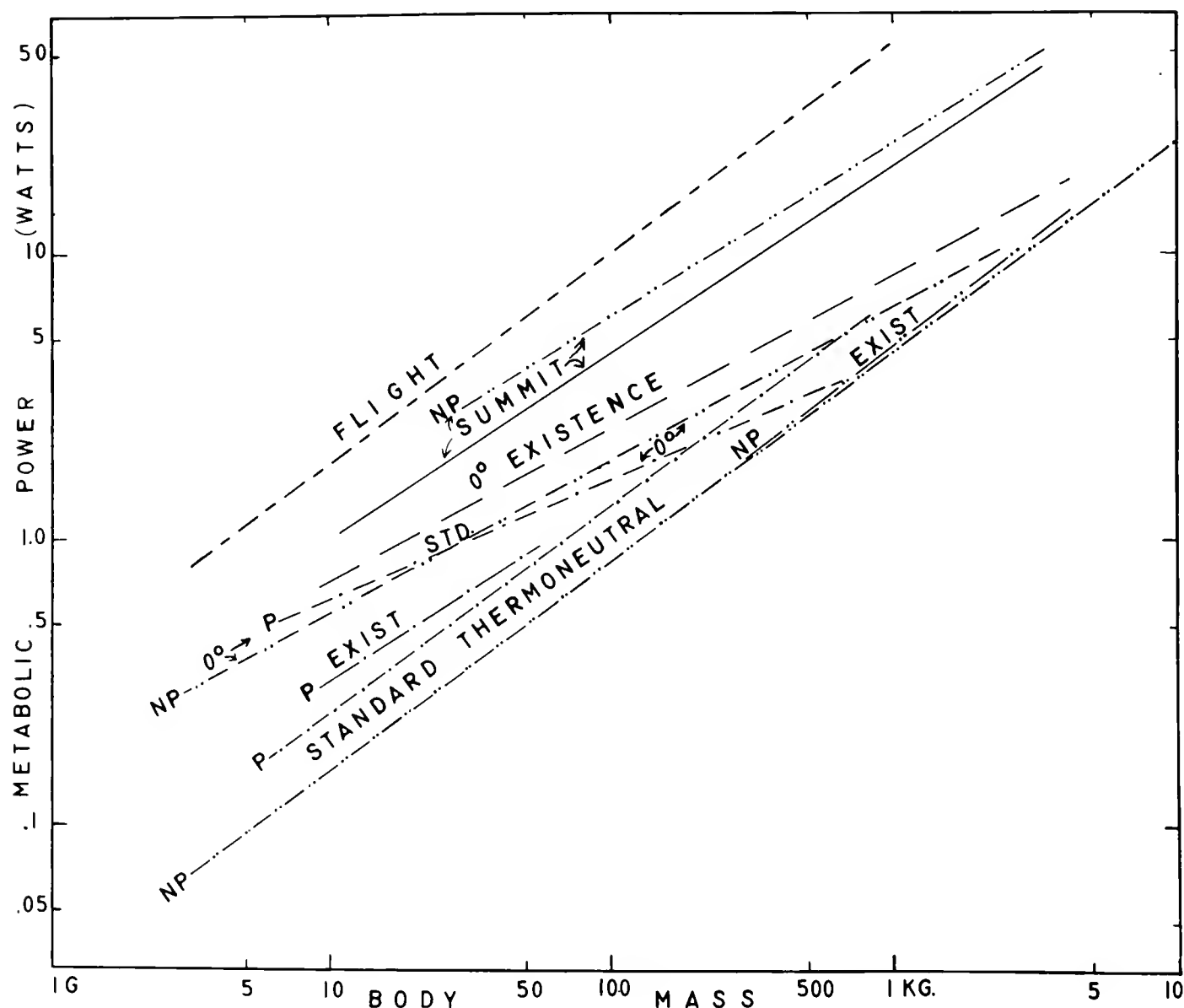


FIG. 7. A comparison of allometric regressions for metabolic power under various conditions. (See text, equations 6, 13, 5, 12, 31d, 31c, 14, 38, 37, and 39, from bottom to top.)

With conversion to SI units, Kendeigh's (1969) expressions for standard metabolism may be substituted into equation (31) as follows (see Fig. 7).

$$\text{Passerines: } \dot{H}_{m,0^{\circ}}, \text{ mWatts} = 230.9 m^{0.42} = 5.29 m^{0.46}(40^{\circ} - 0^{\circ}) \tag{31c}$$

$$\text{Nonpasserines: } \dot{H}_{m,0^{\circ}}, \text{ mWatts} = 161.8 m^{0.53} = 4.72 m^{0.46}(40^{\circ} - 0^{\circ}) \tag{31d}$$

Note that the exponents on the right side are reasonably similar to those derived by Kendeigh, the differences (referred to as *residual mass exponents*, RME; Stahl, 1967) being: -0.04 and 0.07 .

Summit vs. Exercise Power

Since the exponent for \dot{H}_m is much smaller for \dot{H}_m at 0°C than in the thermoneutral range, it would be of interest to examine \dot{H}_m allometrically at still lower temperatures especially in view of the fact that T_{lc} for some birds may be below 0°C (Kendeigh, 1969). The

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summit metabolism (\dot{H}_{\max}) is the maximum heat production, at a temperature below which the bird would be unable to maintain T_b and metabolism would then drop from the Q_{10} effect. Some data for the summit metabolism of birds were obtained by Giaja (cited in Brody, 1945). For Giaja's four species of nonpasserine birds ($p < 0.001$; 30 to 3450 g. body mass):

$$\text{Nonpasserines: } \dot{H}_{\max} = 21.65 M^{0.60}, \text{ in Watts, or} \\ 373.8 m^{0.60}, \text{ in mWatts} \quad (37)$$

When we include the above nonpasserines with his three species of passerines (13-30 g) plus seven species from more recent literature, 11 to 72 g body mass, exposed to -20°C to -50°C , ($p < 0.001$):

$$\text{All birds: } \dot{H}_{\max} = 20.16 M^{0.65}, \text{ in Watts, or} \\ 221.3 m^{0.65}, \text{ in mWatts} \quad (38)$$

The data for \dot{H}_{\max} are limited and were not all obtained at the same T_a , so it is not clear whether the steeper slope than for Kendeigh's H_m at 0° expression is meaningful or not.

How does \dot{H}_{\max} compare with the heat production during the physical activity of flight? Hart and Berger (1972) have derived an expression for oxygen consumption in flight for all birds measured, converted to heat production, assuming $20.1 \text{ j (mlO}_2\text{)}^{-1}$:

$$\dot{H}_{\text{flight}} = 52.88 M^{0.73} \text{ (in watts) or } 341.4 m^{0.73} \text{ (in mWatts)} \quad (39)$$

However, the data used for this derivation were collected under diverse conditions, some of brief duration, and may not be fully comparable. Pennycuik (1969) gives a theoretical exponent of $m^{1.17}$. Tucker (1973, eqn. 57-59) derived approximate equations for power input at the speed of minimal transport cost as follows:

$$\dot{H}_{\text{flight}} = 84.7 m, \text{ for average wingspans} \quad (39a)$$

$$\dot{H}_{\text{flight}} = 67.3 m, \text{ for 120\% of average wingspan} \quad (39b)$$

$$\dot{H}_{\text{flight}} = 113 m, \text{ for 80\% of average wingspan} \quad (39c)$$

We can use equations 39 and 39a to compare the energetics of flight and summit metabolism (Fig. 7). Differences in exponents mean that the ratio of flight to summit metabolism will vary with body size, but from the available data, a flying 30 g nonpasserine bird can metabolize 0.96 to 1.31 times as intensely as when perching and shivering, and a 1 kg nonpasserine, 2.44 to 3.91 times as intensely. Comparable ratios for all birds are 1.23 to 1.87x for a 30 g bird, and 2.62 to 4.20x for a 1 kg bird. Thus, it seems that more heat can be produced in the overt flight movements than by shivering. However, the heat transfer by forced convection is increased by an even greater factor, 5 to 5.8 for flying Budgerigars (*Melopsittacus undulatus*) and Laughing Gulls (*Larus atricilla*) (Tucker, 1972). So it appears unlikely

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that a bird can thermoregulate in sustained flight exposed to a temperature that would evoke summit metabolism when perched.

Bergmann's Rule and Energetics

Thus far we have considered the *energetic consequences* of body size for birds. We have seen that the metabolic requirements in thermoneutrality, at 0°C., in summit metabolism, and in flight are functions of a fractional power of body mass ($m^{0.72}$ to 0.73 , $m^{0.42}$ to $m^{0.53}$, $m^{0.60}$ to 0.65 , and $m^{0.73}$, respectively; Fig. 7). The logistics of supporting the metabolism may be tentatively analyzed as the product of capacity ($\propto m \sim 1.0$), frequency ($\propto m^{1/4}$ to $1/3$) and fractional utilization ($\propto m^0$). Waste heat is lost, at least in controlled laboratory conditions in proportion to the product of the temperature difference, $T_b - T_a$, and the heat transfer coefficient. Now let us examine the possible *energetic advantages* of body size.

What are thought to be the advantages of body size are usually associated with one of the ecogeographical rules, Bergmann's Rule. The widely accepted views are summarized by Mayr (1963): ". . . Bergmann's rule states that 'races from cooler climates tend to be larger in species of warm-blooded vertebrates than races of the same species living in warmer climates' . . . The validity of these empirical findings is independent of the physiological interpretation given to the observed regularities." That distinction is a very important one. The physiological interpretation is that heat is lost via the body surface, the area of which is proportional to linear dimensions squared or $m^{2/3}$, while heat is produced and stored in the body volume (l^3 or $m^{1.0}$). Therefore, the surface to volume ratio would decrease with increasing body mass ($m^{2/3} \cdot m^{-1} = m^{-1/3}$), which is taken to be a *relative* advantage for heat retention.

It is unnecessary to reiterate the well-known debate concerning Bergmann's rule (Scholander, 1955, 1956; Mayr, 1956, 1963; Irving, 1957). More recently, there have been several significant contributions to the interpretation of this rule. James (1970) re-read Bergmann's original paper and found that the rule was originally conceived as applying to interspecific differences (intrageneric), not intraspecific size differences. However, James (1970) and Johnston and Selander (1971) elegantly document the existence of intraspecific climate-related size trends.

The allometric exponents for interspecific metabolic power as a function of body mass are smaller at 0°C. than in thermoneutrality (see equations 5, 6, 12, 13, 14, 31a, b, c, d). This means that the metabolism increases proportionally more for the smaller birds going from thermoneutrality to 0°C. Kendeigh (1969) made several conclusions from this allometric analysis, including: "Increased size appears of obvious physiological advantage for tolerating cold in several ways: (1) reduction in relative amount of energy required for existence, (2) lower metabolic stress per degree drop in temperature,

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(3) extension of zone of thermal neutrality to a lower critical ambient temperature. . . ." He also pointed out that any physiological benefits of larger size could confer ecological disadvantages because of greater food requirements.

The linear equation (31) conveniently approximates the total, steady-state, heat loss of a bird within the limited range of conditions of a metabolic chamber. Recently there has been considerable discussion and debate concerning the proper name, origin, and uses of this model of Scholander, et al. (1950). (See McNab, 1970, 1973; Strunk, 1971, 1973; Kleiber, 1972b, 1973; Tracy, 1972, 1973; Calder and King, 1972; and Bakken and Gates, *in press* and MS.) Clearly, this model from an unnaturally simplified environment has provided an indispensable basis for comparing thermal responses of birds from different habitats, phylogenies, and body sizes, in which role it will continue to serve and stimulate. However, extrapolations cannot be made from the metabolic chamber to the field (see Tracy, 1972) nor does it describe any "law" of heat exchanges. Reference to the model as Newton's Law is a figment of the biologists' oversimplification (the Newtonian Figment) and Fourier only intended his law to apply to conductive heat transfer, not convective and radiative exchanges which are non-linear. Forthcoming papers of Bakken and Gates (*in press* and MS) will clarify this.

Hence, the following analysis will follow the "electrical analog of heat flow" (equation 31) as has been applied to data from metabolic chambers wherein the overall heat transfer coefficient describes heat transfer in a uniform environment with temperatures of the air and the chamber walls all assumed to be the same. This heat transfer coefficient (h) can theoretically be broken down into three factors of more specific physical dimensions:

$$h = \lambda SL^{-1} \quad (40)$$

where λ = heat conductivity (mWcm^{-2} per cm thickness), S = surface area (cm^2), L = thickness of insulating layer (cm). Substituting in eqn. 31, we have:

$$\dot{H}_m - \dot{H}_e = \lambda SL^{-1}(T_b - T_a) \quad (41)$$

Biologists do not usually measure S or the highly variable L , λSL^{-1} usually being lumped together as "conductance" = h , heat transfer coefficient ($\text{mW}^\circ\text{C}^{-1}$, formerly $\text{cal (g hr }^\circ\text{C)}^{-1}$ (see below). Until measurements prove otherwise, we might assume that λ of bird feathers (keratin plus air spaces) and of bird flesh is independent of size, although the thickness and area may vary.

It is usually argued that the thermal disadvantage of small size is the greater surface:volume ratio. However, the larger the bird, the greater the surface area, and therefore a greater heat loss. If the conductivity of bird flesh and of feathers is independent of body size, as is body temperature, then the main advantage of greater size is the

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length of the path for heat loss, which for a given difference of ($T_b - T_a$) will give a more shallow gradient. For example, a larger bird will have greater surface area (equation 34) for heat loss than a small bird, though not as much per g body weight.

Thus since L should be proportional to $m^{0.25}$ to $m^{0.33}$ (see McMahon, 1973), we can substitute (34) in (40):

$$h = \lambda SL^{-1} \propto \lambda m^{0.67} m^{-0.33} \propto \lambda m^{0.33} \quad (42)$$

$$h = \lambda SL^{-1} \propto \lambda m^{0.67} m^{-0.25} \propto \lambda m^{0.42} \quad (42a)$$

Kleiber (1972a) stated: "Our result that the basal metabolic rate increases with the $\frac{3}{4}$ power of body weight but heat conductance increases only with the square root of bodyweight may serve as an explanation of Bergmann's rule that cold climate favors big animals."

Since $h \propto m^{0.46}$ (equations 32, 33), we can solve for λ :

$$\lambda \propto m^{0.46} m^{-0.33} = m^{0.13} \quad (43)$$

$$\lambda \propto m^{0.46} m^{-0.25} = m^{0.21} \quad (43a)$$

which is not what we expected, above, but similar to what Birkebak (1966) found for the fur of mammals, that is, the specific conductivity decreases with size; larger feathers make poorer insulation. Furthermore, it suggests the desirability for specific thermal conductivity measurements of feathers, which probably constitute the major component limiting the heat transfer coefficient for birds. Brody (1945: p. 626, 639–640) analyzed Wetmore's data on feather weights in passerine birds and found that feather weight was linearly related to body mass. However, expressed as a function of body surface area, it becomes obvious that the amount of insulation per cm^2 of surface increases with body mass (δ :0.0075 $m^{0.26}$; ϕ :0.0060 $m^{0.32}$).

Thus far we have found two possible advantages to larger size: (1) thermoneutrality extends to lower temperatures and (2) a reduced heat transfer coefficient (a composite of thicker or heavier feather layer per cm^2 surface, less surface area per g body mass, and specialized layers possible on larger birds). Considered as isolated factors, these would seem to make a compelling case for a physiological significance to Bergmann's rule.

Nevertheless, McNab (1971) rightly points out that we must consider the biological unit of the whole animal, whose *absolute* heat loss, from an *absolutely* larger surface area, is greater, and whose food requirements are also greater, the larger the descendants become, *relative* reduction of surface area notwithstanding.

The best way to grasp this is to examine some values. I have assumed that $T_b = 40^\circ\text{C}$ (Calder and King, 1974), and calculated the rates of heat loss from equations (5), (6), (32), and/or (33), as appropriate, using values for body mass reported for various birds (Table 2). It is obvious that in every case, the larger bird loses absolutely *more heat*. Perhaps the real birds selected represent too small a size range, so

TABLE 2
The Effect of Increasing Body Size upon Total Heat Loss Rate.

Species	Location	Body mass (g)	Source	Assumed T _a (°C)	Heat loss rate (mW)
Downy Woodpecker	26° N	25.5 ¹	James, 1970	0	894.6
Downy Woodpecker	44° N	27.2 ¹	James, 1970	0	921.4
Downy Woodpecker, ♀	Georgia	21.3	Norris and Johnston, 1958	0	821.3
Downy Woodpecker, ♀	Ohio	24.8	Norris and Johnston, 1958	0	882.5
Black-capped Chickadee, ♂	Ohio	10.0	Baldwin and Kendeigh, 1938	0	629.8
Black-capped Chickadee, ♂	Alaska	11.1	Irving, 1960	0	661.3
Carolina Chickadee	Georgia	9.4	Norris and Johnston, 1958	0	611.9
Carolina Chickadee	Ohio	10.6	Norris and Johnston, 1958	0	658.8
Cardinal	Florida	37.8	Norris and Johnston, 1958	0	1172.6
Cardinal	Ohio	41.2	Norris and Johnston, 1958	0	1220.9
Hypothetical passerine	Louisiana	25.0	This study	thermo-neutral	372.27
Hypothetical passerine	Yukon	50.0	This study	thermo-neutral	617.46
Hypothetical passerine	Louisiana	25.0	This study	0	966.3
Hypothetical passerine	Yukon	50.0	This study	0	1336.8

¹ From second equation of James, 1970, p. 385.

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consider a 25 g hypothetical passerine, and a relative that evolved to twice that size. A 100% increase in body mass requires a smaller (66%) increase in basal (thermoneutral) metabolism, and a still smaller increase (38%) in 0° metabolism. Just as Kendeigh (1969) indicated, the larger bird would require absolutely more food. It is true that each additional gram of body mass becomes progressively less expensive, but since there is some finite increment of expense, the Bergmannist is left with a question to answer: Why add another gram? As McNab pointed out, there is no mechanism known that could tell a bird that it was saving $100 - 66 = 34\%$, only that its cost had gone up 66%. Its territorial requirements also increased 100%.

There must be some advantage, but what is it? One possibility may be fasting endurance. There are times in inclement weather, overnight, during migration, or in scarcity or famine, when birds are temporarily unable to feed. The amount of energy reserves and the rate at which they are consumed will together determine how long a bird can survive:

$$\text{duration of reserve} = \frac{\text{amount in reserve}}{\text{rate of consumption}} \quad (44)$$

I have selected maximum values for mass of fat and body mass for 19 passerine birds from reports by Odum (1960), Helms (1963), King and Wales (1965), and Johnston (1966) and find that:

$$\text{Fat mass} = 0.03 \, m^{1.57}, \quad (12.4 \leq m \leq 41.3; \quad r = 0.71, p = 0.001) \quad (45)$$

while 3 nonpasserines from Odum, et al. (1961) are summarized:

$$\text{Fat mass} = 0.06 \, m^{0.83}, \quad (5 \leq m \leq 72; \quad r = 0.99, p = 0.001) \quad (46)$$

Substituting these power functions in equation (44):

$$\text{Passerines, thermoneutrality: duration} \propto m^{1.57} \div m^{0.72} = m^{0.85} \quad (47)$$

$$\text{Passerines, } 0^\circ\text{C: duration} \propto m^{1.57} \div m^{0.42} = m^{1.15} \quad (48)$$

$$\text{Nonpasserines, thermoneutrality: duration} \propto m^{0.83} \div m^{0.73} = m^{0.10} \quad (49)$$

$$\text{Nonpasserines, } 0^\circ\text{C: duration} \propto m^{0.83} \div m^{0.53} = m^{0.30} \quad (50)$$

These represent the most crude approximations, but they all suggest that the larger the bird, the longer it can survive fasting, especially during cold stress. Kendeigh (1945) lists survival times without food for various birds at comparable temperatures. Least-squares regression analysis gives the following expressions:

$$\text{Survival time, hr, at } -13 \text{ to } -18^\circ\text{C} = 3.70 \, m^{0.59};$$

$$r = 0.953, S_b = 0.140, S_{yx}(\log) = 0.057 \quad (44a)$$

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Survival time, hr, at -1 to $-9^{\circ}\text{C} = 5.42 m^{0.58}$;

$$r = 0.959, S_b = 0.160, S_{yx}(\log) = 0.077 \quad (44b)$$

Survival time, hr, at $+2$ to $+6^{\circ} = 24.34 m^{0.39}$

$$r = 0.795, S_b = 0.279, S_{yx}(\log) = 0.095 \quad (44c)$$

In studies of flight, migratory reserves have been assumed proportional to body mass ($m^{1.0}$). Hart and Berger (1972) stated that \dot{H}_{flight} is proportional to $g^{0.73}$ (equation 39). Again substituting in (44) we find:

$$\text{duration} \propto m^{1.0} \div m^{0.73} = m^{0.27} \quad (44d)$$

The reader is reminded of the limitations of eqn. (39) discussed above. Thus larger body size again may confer an advantage of endurance. The bird exposed to a long, cold night must have enough stored energy to resume foraging when the opportunity comes again, as James King pointed out in the previous chapter.

The fasting-endurance hypothesis to explain the trends of Bergmann's Rule has been suggested previously by Lindsey (1966) and Rosenzweig (1968). Regarding the body sizes of poikilothermic vertebrates, Lindsey stated: "During winter shortages the energy reserves may last longer in large than in small animals, since basal metabolic requirement per unit weight is often less in larger individuals." Rosenzweig listed homeostasis as one of seven hypotheses to explain Bergmann's Rule, body size "as a homeostatic device to overcome short-term fluctuations in, or low winter levels of, food supply."

SUMMARY OF GENERAL AND THEORETICAL TREATMENT

To this point, several conclusions (C) and guesses (G) have been made:

1. (C) The smaller the bird, the lower its total metabolic power, but the higher its metabolic power per gram body mass.
2. (C) The dependency of thermoneutral metabolic power on $m^{0.72}$ to 0.73 is parallel, but higher for passerine vs nonpasserine birds, higher for α -phase than ρ -phase in the circadian cycle and higher in flight compared to resting.
3. (C) The ΔT at lower critical temperature is a function of $m^{-1/4}$. Consequently, at temperatures below the size-dependent thermoneutral range, the metabolic power body mass exponent is less than the $m^{3/4}$ observed in thermoneutrality.
4. (G) Supply or delivery functions can be described as the product of a capacity ($\propto m^{1.0}$), a frequency of drawing that capacity ($\propto m^{-1/4}$), and a fractional utilization term that is probably size independent (m^0). The product of these is the metabolic consumption rate.

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5. (G) Maximum energy reserves are possibly linearly proportional to body size, but the rate at which they are metabolized increases as a less-than-linear function of body weight. Consequently, the smaller the bird, the more rapidly its reserve margin will be expended.
6. (G) From various approaches, the bird's physiological time is a proportional $m^{-1/4}$. In other words, lifespan, cardiac cycle, and period of turnover per kilojoule of energy or per liter of oxygen all increase with increasing body size (bigger lasts longer).
7. (G) On the other hand, earth-time stands still for no bird, so behavioral and other nonallometrical factors must come into play in coupling physiology and environment.

Now, having surveyed in generalities the influence of body size on avian energetics, let us turn to the small end of the body size spectrum, where Dr. Lasiewski did so much interesting research, to see how the natural history of hummingbirds fits the preceding conclusions.

BODY SIZE AND HUMMINGBIRD ENERGETICS (THE NEW TROCHIDOLOGY)

A physiological ecologist seeks to explain how the animal can cope with environmental factors, e.g. temperature extremes, aridity, hypoxic stress. Filled with "gee-whiz" facts and notions about surface/volume ratios and established allometric equations, one is particularly impressed with the success of hummingbirds (Family Trochilidae) at the small end of the spectrum of body size. As yet, there are no physiological data on the smallest species of bird, the Bee Hummingbird (*Calypte helenae*; body mass 2 g; Austin, 1961).

The small hummingbirds have the highest surface-to-volume ratios, the highest "per-gram" heat transfer coefficients (thinnest insulation), the most intense metabolism per g body mass, the highest heart, respiratory, and wingbeat frequencies of all birds (Lasiewski, 1963a, 1964; Lasiewski and Lasiewski, 1967; Lasiewski, et al., 1967; Calder, 1968; Berger and Hart, 1972). Bergmann's Rule as commonly interpreted before McNab's (1971) clarification would imply that the high surface: volume ratio should discourage small hummingbirds from occupying chilly habitats. However, the hummingbird with the most northerly distribution (61°N; Bent, 1940) is *Selasphorus rufus* which weighs only 3.1 to 4.8 g. *Stellula calliope* is the smallest hummingbird of temperate North America (2.6-3.0 g) but in the Rocky Mountains it does not breed south of Wyoming and Utah. *Archilochus anna* (3.4-5.4 g) remains farthest north in winter, and is the only breeding bird in the California chaparral in the cooler winter months (Stiles, 1973). This in itself suggests that we have exaggerated notions about the liability of small body size during "coldstress." In contrast, *Eugenes fulgens* (6.6 g) and *Lampornis clemenciae* (7.9 g) breed in southeastern Arizona, only rarely wander farther north, and do not remain in Arizona for the winter (Bent, 1940; Baker and Blake, 1962; Bartol, 1973; body masses

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from Lasiewski, 1963a; Phillips, et al., 1964; Lasiewski, et al., 1967; Lasiewski and Dawson, 1967). Small *Sephanoides sephanoides* breeds at the highest southern latitude of any hummingbird. Altitudinally, *Selasphorus flammula* (2.4-3.0 g) breeds to 3,200 m in Costa Rica (Hainsworth and Wolf, 1972c). However, the largest, *Patagona gigas* (19.1 g) also dwells in the high Andes (Lasiewski, et al., 1967). Thus, if Bergmann's ecogeographic rule has thermoregulatory significance, it hardly seems to have influenced enough hummingbirds to provide a consistent trend.

If they are regarded as whole birds rather than weight specific entities, hummingbirds have the lowest total "basal" (standard) metabolic rates, the smallest surface areas for heat loss, and the lowest total heat-transfer coefficients of any birds. These factors and their ability to hover enable them to subsist on tiny insects and on minute quantities of nectar per flower visited. The energetic cost of transporting a hummingbird vertically is slight, relative to resting metabolism, so that they can probably fly up to high elevations for feeding when lowland flowers have declined in nectar production, then to retreat from inclement weather by returning to lower elevations (see observations of Swan, 1952; Smith, 1969). This situation is probably similar to that of mammals running up and down hills. Taylor, et al. (1972) showed that relative to its basal expenditure, the increment for a 30 g mouse to run up an incline was one-eighth that for a 17.5 kg chimpanzee.

Nevertheless, the relationship between energy storage capacity and rate of consumption gives them the shortest durations for the development of an "energy crisis" (equation 44). Hainsworth and Wolf (1972a) estimated that the metabolism of a 3 g hummingbird could be supported for ca. one-half hour of flight or 1.4 hr of resting at 10°C by the energy content of a full crop of 0.5 M sucrose. Subsisting on nectar of 1.0 M sucrose, the full crop would fuel 4.2 hr of rest at 20°C. If hummingbirds have little margin to spare in attaining energy balance, we might expect mechanisms for energy conservation and extraction to be well-developed. Feeding mechanisms and behavior should have been optimized for exploitation of available resources. Time budgets should reflect maximum use of available daylight feeding time, in preparation for the nocturnal fast. Roosting sites, nest location, and materials should be selected to reduce heat loss and therefore the energetic cost of thermoregulation. If the metabolic requirements of homeothermy threaten to encroach on the reserves needed to return to a food source at daybreak to resume feeding, the thermostat should be set to a lower level, requiring less energy (Pearson, 1953).

FOOD EXTRACTION

The nectar drinkers "provide one of the most remarkable instances . . . of the dependence of a bird's season of reproduction on the food

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supply . . . in defiance of apparently inimical features of the climate" (Skutch, 1950). Skutch observed that Central American hummingbirds nested mostly at the onset of the dry season (November to February at various locations) when sunny skies combine with recent moisture in bringing the greatest profusion of flowers. Stiles (1973) has analyzed in detail the relationship between the food supply and the annual cycle of Anna's Hummingbird.

Indeed, the territory of a male hummingbird centers on a food supply, which may serve secondarily as a mating station (Pitelka, 1942; Wolf and Stiles, 1970). Vigorous, food-centered territoriality persists during the nonbreeding season in resident Anna's Hummingbird (Stiles, 1973) and during migration of the Rufous Hummingbird (Armitage, 1955; Dunford and Dunford, 1973).

Wagner (1946) outlined three stages in the evolution of the food habits of hummingbirds: (1) the onset of the exploitation of nectar sources following an insectivorous ancestry; (2) adaptation to year-round reliance upon nectar as the major food source; and (3) resumed utilization of insects and (or) migration with the more seasonal climates of the late Tertiary (especially those hummingbirds which had colonized Subtropical and Temperate Zones where nectar became cyclically unavailable).

Feeding from both flower nectar and small insects is usually accomplished while the hummingbirds are hovering. The power input of hovering is costly, 6.7 times the standard metabolism ($14.5 \dot{H}_{sm}$) for a 10 g *Eulamparis jugularis*, $14 \dot{H}_{sm}$ for *Amazilia fimbriata* (5.7 g), and $15.1 \dot{H}_{sm}$ for a 3 g *Calypte costae* (Wolf and Hainsworth, 1971; Berger and Hart, 1972; Lasiewski, 1963a).

Obviously, the energy intake must exceed the energy cost of hovering or there would be no incentive to pollinate the flowers. The rates of oxygen consumption during hovering for the three species cited above were 42.4 to 43.4 ml O₂/g hr. Assuming an energetic equivalent of $20.1 \text{ j}(\text{ml O}_2)^{-1}$ we find that the power input for hovering is:

$$\dot{H}_{\text{hov/g body mass}} = 231.6 m^{0.019} \text{ mW}(\log S_b = 0.0012; S_m = 0.0016) \quad (51)$$

$$\dot{H}_{\text{hov}} = 231.6 m^{1.019} \text{ mW} \quad (51a)$$

Thus these limited data indicate that the energy cost of hovering per g appears to be almost independent of body size. Hainsworth and Wolf (1972b) concluded the same from theoretical analysis, but Epting and Casey (1973) point out that the power requirement per gram for hovering is a function of wing disc loading, and that the apparent size-independence of power/g is the result of a fortuitous similarity in wing disc loading for the three hummingbirds studied thus far. From determinations of nectar concentration and extraction rates, Wolf et al. (1972) and Hainsworth and Wolf (1972c) have expressed the relation of foraging cost to energy uptake during nectar feeding, e.g., for *Selasphorus flammula* (2.8 g) feeding at *Tropaeolum* blossoms as:

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$$\text{Foraging cost (cal.)} = 0.01 + 0.09 \times (\text{nectar intake, cal.}) \quad (52)$$

The 0.01 intercept can perhaps be regarded as a "down payment" or the insertion cost. Beyond that, 9% of the energy yield is spent in hovering while extracting the nectar. Five combinations of three lowland hummingbird species and three species of *Heliconia* flowers yielded expressions with higher insertion costs (0.21 to 0.47) and a range of 4 to 11% of the intake as cost of hovering. The remainder of 89 to 96% of the energy intake is available for flying to and from the flowers, defending the territory, nesting, and in support of physiological homeostasis.

How many flowers would a hummingbird visit in a day, and thus pollinate? Hainsworth and Wolf (1972c) made estimates for *Selasphorus flammula* feeding from a species of *Salvia*. They estimated thermoregulatory requirements using h predicted from Herreid and Kessel's (1967) equation (similar to equation 32 of the present paper), assumed $T_b = 41^\circ\text{C}$, average $T_a = 15^\circ\text{C}$, 20% of the 12.5 hr day spent foraging and 80% spent at 1.7 times basal. From their measurements of nectar concentration and replacement, they estimated that 1,565 different flowers would be required to meet daytime energy requirements (at 313 flowers/hr revisited about once each 5 hr). A nesting female's nocturnal metabolism (average $T_a = 5^\circ\text{C}$) was estimated to require 1,100 flowers, which contribute to a 24-hr minimum of 2,700 flowers (540 per daylight hour; assumptions about heat conservation due to insulation of nest not stated).

Reflection on equations (51a) and (52) suggests that with increasing body weight the total power requirement of hovering would eventually exceed the rate of energy intake from a flower of a given nectar volume and concentration. Hainsworth and Wolf (1972b) pointed out this upper limit to body size for hovering and cited the example of *Eutoxeres aquila* (10-11.5 g) which perches while feeding from *Heliconia rostrata*. Thus nectar production and structure of inflorescence can exclude larger birds from utilizing and pollinating a species of flower. On the other hand, Hainsworth (1973) also found that the rate of nectar intake is greater for 27.9 g *Lampornis clemenciae* than for an *Archilochus alexandri* weighing 3.0 g by a factor similar to that of their body masses and therefore their hovering costs.

One would not expect a 20 g bird to hover while feeding on flower nectar unless there were very large flowers with sufficiently copious nectar production to pay the cost of hovering and provide a reasonable energetic profit. The "cultural evolution" of hummingbird feeders has provided the incentive for House finches (20 g *Carpodacus mexicanus*) to learn to hover for 1-5 sec of stationary feeding beneath a feeder spout (Taylor, 1972). This interesting behavior was learned by adults in two weeks, by immatures in six weeks. Taylor observed 8,971 drinks by 20 individuals in 458 hr, which suggests strongly that it is energetically profitable. At the peak of drinking, the finches

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averaged 140 drinks/day, from which Taylor calculated that they were drinking 12% of their body mass in sugar. From this amount, 39.54 kJ of energy or 1.14 times the standard metabolism for one day (equation 5) would be derived from drinking at the feeder in addition to food from other sources.

TIME ALLOCATION

"Time is money" to the businessman. Man has interposed an artificial medium of exchange between time and energy. His time must be converted to profits or wages, and these can then be exchanged to meet his real or imaginary energy requirements. The value of money is variable and not consistently related to the value or scarcity of the energy resource, hindering our ability to cope with energy shortages.

In nature, the bird must convert its time directly to energy. If the conversion is inefficient, the bird may not attain energy balance (Fig. 8). Therefore, the way in which the hummingbird utilizes its time or couples its rapid physiological time scale to the cycles imposed by the earth's rotation and revolution is of great importance. Survival of the nocturnal fast and perpetuation of the species hinge upon these temporal relationships. Information on daily time-related behavior is of direct interest in itself, and can also be used to estimate the energy



FIG. 8. This hummingbird has attained equilibrium and mummified, apparently an instance of natural selection against those who do not succeed in attaining energy balance. Note ptiloerection which has been preserved, evidence of the last effort to conserve energy. Found beneath a shale overhang above La Cañada del Oro, elev. 1,220 m in Santa Catalina Mountains, Arizona, by W. A. Calder, IV.

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budgets of hummingbirds (see below). Similarly, timing is of interest with regard to the exploitation of seasonally available nectar sources.

Daily Cycle

In a 24-hour scale the life of the hummingbird is divided energetically, into two contrasting phases which are characterized by feeding and fasting. A positive energy budget must be attained during daylight activity to provide a reserve for the nocturnal fast. During that fast, energy expenditures must be at rates that will spare sufficient energy to resume feeding the following day.

This nocturnal energetic cost will be a function of the nesting or roosting microclimate, the body temperature being maintained (normothermic or hypothermic) and the length of the night.

Regarding the problem of hummingbirds who must support high metabolic intensity over long nights in cold climates, Pearson (1953) considered four courses to energy balance: (1) feeding before dark, (2) feeding at night, (3) retreat to warmer places, and (4) torpidity. Of the first two, which involve energy intake, hummingbirds do not feed at night. This leaves only intense feeding before dark and resumption of feeding at the first adequate daylight intensity.

As was discussed above (pp. 110-116; equations 44-50), the smaller the bird, the shorter the period of fasting which it can endure. The period of fasting imposed upon the bird is a function of season and latitude. At a given latitude, the nocturnal phase is longest at the winter solstice, and shortest at the summer solstice. In the summer the ratio, feeding time/fasting time, increases with latitude, while it decreases with latitude in the winter. The similarly-sized Broadtailed Hummingbird (*Selasphorus platycercus*) breeding in the summer at high elevations in Colorado and the Anna Hummingbird (*Archilochus anna*; see Mayr and Short, 1970) breeding in late winter in southern Arizona may face similar temperatures, but the Broad-tail has 62% of the 24 hrs in which to feed, the Anna only 48% (see Table 3).

The available daylength decreases after the summer solstice, which means a decrease in the margin above the minimal amount of time required for foraging. This would seem to place an advantage in timing hatching to coincide with the longest available daylengths for feeding (see discussion of annual cycle of the Broad-tail in the nest section). That an Anna Hummingbird could succeed in rearing young with considerably shorter days makes it obvious that many other factors such as competition and local food supply are involved.

Thus it appears tentatively that within a stage (incubation or brooding) the total absence or recess time ("inattentive") is similar, regardless of daylength, and that onset of the feeding phase is a function of light intensity. If the day is shorter, a smaller percentage of it can be spent on the nest. The number of feeding trips may be a function of distance to, and quality of, the food supply. The average constancy (% on nest) of five species of hummingbirds in Central America was

TABLE 3
Time and Daylight Utilization by Breeding Hummingbirds¹.

Species	Location/month	Aver. min. air temp. (°C.)	Active daylength (min.)	Minimum light intensity	Recesses per day ⁶	Total absence (min.)	Constancy % of daylength
INCUBATING FEMALES							
Calliope	Wyo./V-VI	4.4	967	--	99.5	216.6	77
Broad-tail	Colo./VI-VII	1.4	887	6.2 ± 3.47	90.6(60.1)	190.8	78
Anna's	Ariz./II	4.0	689	39.3 ± 21.81	33	210.3	69
Anna's ²	Calif./IV	10.0	843	--	65	173	79
Black-chin	Ariz./IV	11.0	804	--	65.4(49.6)	--	--
BROODING FEMALES							
Calliope	Wyo./VII-VIII	4.7	974	--	84.1	306.6	67
Broad-tail	Colo./VII-VIII	3.7	890	5.9 ± 2.92	83.4(59.8)	330.6	62
Anna's	Ariz./II	5	701	6.1 ± 3.67	53 (38)	328.4	53
Anna's ²	Calif./V ⁶	--	838	--	40	117	86
FEMALES--BREEDING SEASON; STAGE NOT SPECIFIED							
Ruby-throat ³	Sask./VII-VIII	--	1030	--	--	--	--
FEEDING--TERRITORIAL MALES							
Anna's	Ariz./X-II	-7	658	99.2 ± 140.39			
Anna's ⁴	Calif./IX	10.5	772				
BREEDING--TERRITORIAL MALES							
Anna's ⁵	Calif./I	--	639				
Anna's ⁵	Calif./III	--	759				

¹Condensed from Tables 2 and 3 of Calder, MS“b”; ²from data of Howell and Dawson, 1954; ³from Miller and Miller, 1971; ⁴from Pearson, 1954; ⁵from Stiles, 1971; ⁶date of hatching.

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70% (Skutch, 1962). Additional information for higher and lower latitudes would be highly desirable to complete this picture.

Annual Cycle

I have quoted above Skutch's 1950 observation on the dependence of reproduction by nectar-feeders on the food supply. To my knowledge, the only hummingbird for which the testicular cycle has been completely described is the Anna's Hummingbird (Williamson, 1956), about which it was concluded, "Until further evidence is available it seems reasonable to assume that an inherent rhythm is modifiable by rainfall and other factors, such as the presence of females, with the ensuing breeding season occurring in the period when food plants are most numerous." Stiles (1973) suggests "the existence of a photoperiod-sensitive system that regulates the time span during which *anna* males can attain full breeding condition following rainfall." Ruby-throated Hummingbirds (*Archilochus colubris*) arrive near the northern limit of their range in Saskatchewan in late May, nearly a month before flowers are available, feeding on sap from sapsucker holes and on small arthropods (Miller and Miller, 1971).

As an example of a hummingbird advancing to its breeding grounds, establishing territory and nesting in relation to environmental factors, we can consider the Broad-tailed Hummingbird. Bent (1940) categorized this species as "the hummingbird of the Rocky Mountain region . . . it is essentially a mountain bird." As such it encounters and breeds in chilling climates where energy supply might be especially crucial. The Broad-tail returns to the mountains of southern Arizona in late February or early March (24 Feb. 1972; 25 Feb. 1973 in Santa Catalina Mountains) when there is still snow on the ground. Only on warmer slopes are some manzanitas (*Arctostaphylos Pringlei*) beginning to bloom (Philips, et al., 1964; Calder, unpubl.). In early April they arrive in northern Arizona, and from late April to mid-May in Colorado (Phillips, et al., 1964; Bailey and Niedrach, 1965).

In 1973, male Broad-tailed Hummingbirds were heard in Gunnison, Colorado (elev. 2,350 m) on 12 May (unpubl. obser., Mrs. R. E. Richards) and at the Crested Butte Ski Area (2,900 m) on 13 May (Manager, Matterhorn Lodge). Males could be heard and seen flying in Gothic (2,900 m, Rocky Mountain Biological Laboratory) on 16 May when we arrived. The only year-round residents, Mr. and Mrs. George Sibley, had not heard them before they went out for supplies on the 14th. The chronology that followed is depicted in Figure 9, correlated with some environmental observations, mostly qualitative from field notes. Spring, 1973 was late, in terms of initial melt and snowstorms in late May and early June. In contrast, the 1972 season was preceded by an early melt of a light snowpack, said to be the first time since 1934 that the "Old Maid" snow field had melted in half in early August. Data on time of first activity from 1971 and 1972 (Calder, 1974b) also provided a daily time-base for comparison with 1973.

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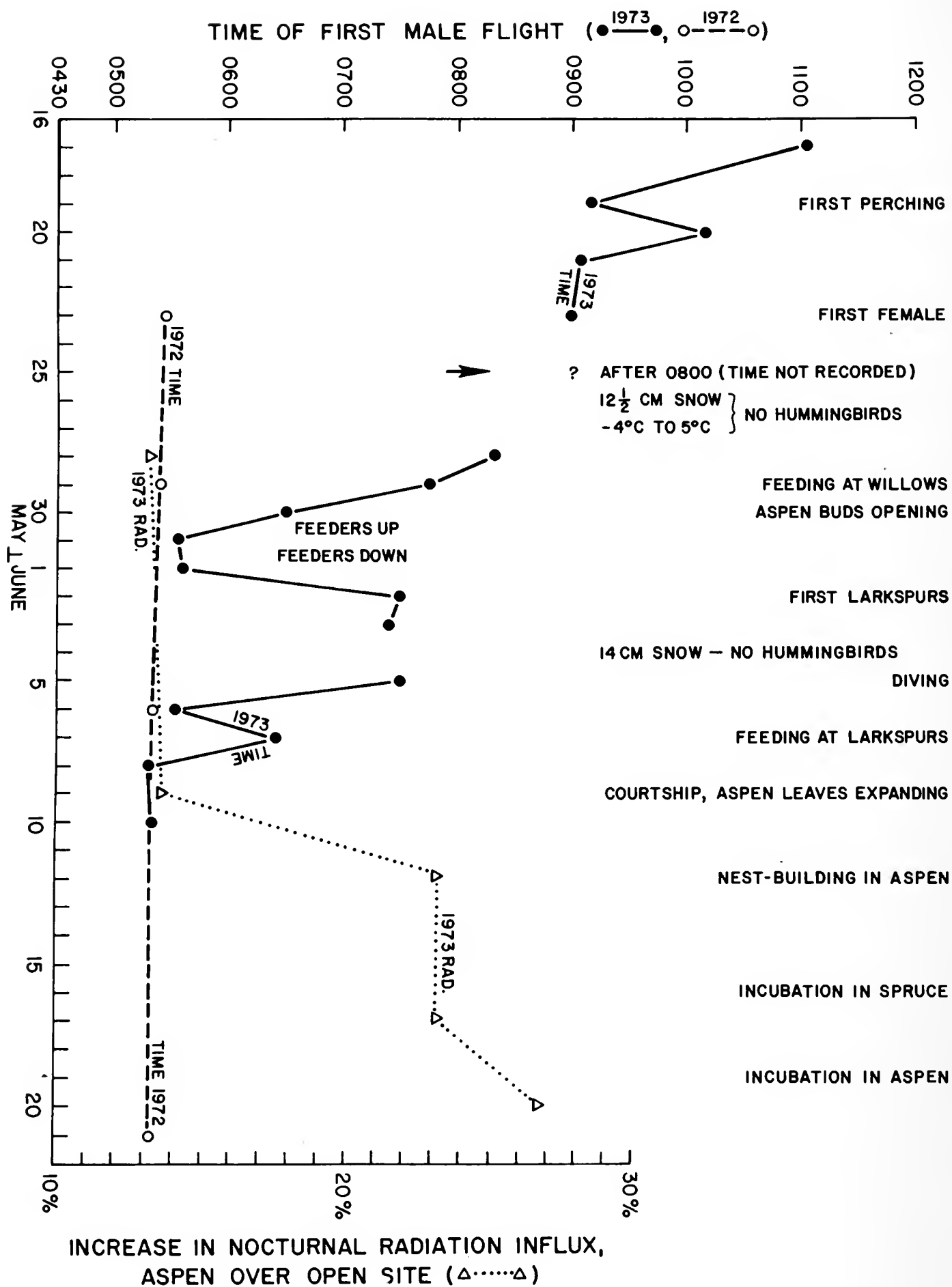


FIG. 9. A correlation of a sequence of environmental phenomena and the onset of territoriality and nesting of male and female Broad-tailed Hummingbirds. (Rocky Mountain Biological Laboratory, 1973. Unpubl. data of W. A. Calder, III and N. Waser.)

Males were first heard and seen 19.8 ± 4.68 (sd) min before sunrise in 1971, 21.7 ± 2.45 (sd) min before sunrise in 1972 (ca. 0522) when territories had been established. In 1973 this did not occur naturally until 8 June, when enough low larkspur (*Delphinium nelsoni*) were

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blooming for feeding. Artificial feeders were up 31 May-1 June which resulted in 0530-0532 onset of activity and territorial display, but these were removed after the brief experiment to allow colonization to be as natural as possible; territorial display and early arrival ceased immediately (Nickolas Waser, 1974). This suggests that the birds were based elsewhere, energetically, making scouting trips up to Gothic until conditions were favorable for energy balance at the ultimate breeding grounds. These observations are similar in the pattern of opportunism noted in daily hummingbird feeding at high elevations in Mexico (Swan, 1952), the territoriality of migrating Rufous Hummingbirds (*Selasphorus rufus*) at nectar sources (Armitage, 1955), and the tie between flowers and breeding discussed by Skutch (1950). By the time that incubation was completed and chicks were to be fed, the days would be decreasing in foraging time available. Thus, there is an obvious advantage to breeding as soon as the local food supply will permit, in addition to the consideration of competition for a nest site.

Courtship and nest-building followed the availability of larkspur and the territorial claiming. Nest building in the aspens can also be correlated with the reduction in radiative heat loss afforded by leaf-out in the aspen stands. Readings from the hemispherical radiometer suspended 0.5 m beneath a nest branch of previous seasons were compared with readings on an open hill nearby. Before leaf-out the aspen trunks and bare limbs provided 13% more long-wave influx than the open sky. When the leaves expanded, increased shielding from the sky resulted in a 23% (at onset of nest-building) to 26% greater influx of long-wave radiation. (Net radiative heat loss by a bird would be the difference between radiation emitted by the bird at its surface temperature and the lesser influx from colder surroundings. The sky temperature at the zenith on clear nights was below -20°C . Any portion of the sky blocked by branches, leaves, and topography would be closer to air temperature (-5 to $+5^{\circ}\text{C}$) and thus would emit more heat to reduce the net loss from a bird.) Incubation followed, beginning 13 days later in spruce and 14 days later in aspen, compared to 1972, but quite similar to dates in 1971.

Once the clutch of two eggs is laid, a total of 34 to 39 days are needed for incubation (15-19 days), brooding (9 to 12 days) and post-brooding to fledging (8-10 days). Renesting or late nesting may be attempted, likelihood of success diminishing with time. A hen who began incubation on 20 July broke Bent's (1940) record for late eggs in Colorado, but the young had to be abandoned, so the effort was in vain. Thus the breeding season continued until energy balance was apparently threatened, primarily by the demise of the nectar-providing flowers but complicated by the arrival of aggressive migratory Rufous Hummingbirds which compete for the remaining nectar in scarlet gilia (*Ipomoxis aggregata*), tall larkspur (*Delphinium barberi*) and paintbrush (*Castilleja* spp.). When energy intake is reduced to the point

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that hen and chicks cannot balance losses, nests with live chicks may have to be abandoned (Calder, 1973c).

Thus the breeding season is, as Skutch (1950) told us, closely tied to the flower supply, with snow melt setting the limit at one end and seeding of flowers and invasion by migrants marking the end for the Broad-tailed Hummingbird. Both ends of the season act as cutting edges for natural selection, to channel breeding into opportunistic exploitation of the earliest possibility for energy balance with high demands of nesting.

TIME-ENERGY BUDGETS

The measurement of standard metabolism in a controlled laboratory environment or of the artificial dietary intake for caged existence is relatively simple. However, the total energy cost of natural life in the wild is almost unknown. The only direct approach devised thus far is the use of doubly-labelled water (D_2O^{18}) turnover, which requires expensive, elaborate equipment and depends upon recapture of the subjects. One alternative which Dr. King discussed (above) is to time various activities at different temperatures and apply the most appropriate steady-state, lab data available to estimate total energy requirements.

Visibility and step-wise activity levels, as well as body size and aesthetic considerations have made hummingbirds useful subjects for time-energy budgets. Hummingbirds do not walk or hop, and the smaller species hover while feeding. Consequently, their time appears divided between six distinct activity levels: torpor, sleeping, sitting in nest (♀ only), perching, flying, and hovering, upon which thermoregulatory demands are superimposed.

Fewer assumptions are involved when simply the time-budgets are compared without estimating energy equivalents. A close similarity is seen in the division of time between perching (sitting) and flying (insect catching, territorial and courtship flight, and foraging) in three species from diverse climates, mediterranean-temperate, tropical, and temperate-montane. The average for the males of these three species (81.6%) is also strikingly similar to the percentage of daytime spent sitting on the nest during incubation of three species of hummingbirds (76%; see Tables 3 and 4, also Skutch, 1962). This also tends to support the idea of energetic equality of the sexes in hummingbirds which are, after all, similar in size on a logarithmic scale!

Pearson (1954) drew up the first time-energy budget for a hummingbird using laboratory values for oxygen consumption during hovering for both forward flight and hovering in the wild. Subsequently more budgets have been estimated for the same species, Anna's Hummingbird, and other species for both sexes at different times in the life cycle and using variations in assumptions (Calder, 1971; Stiles, 1971; Wolf and Hainsworth, 1971; Calder, 1974b: see Table 5). To generalize from what is currently available, it appears that: (1) the total

TABLE 4
Time Budgets of Hummingbirds.

Species	Status	Month	% of accounted time	
			Perched	In flight
<i>Archilochus anna</i> , ♂ ¹	Breeding territory	Jan.	84.0	16.0
	Feeding territory	Mar.	88.4	11.6
	Feeding territory	Sept.	83.0	17.0
	Mean		85.1	14.9
<i>Eulampis jugularis</i> , ♂ ²	Territorial	Jan.	86.9	13.1
	Territorial	Jan.	78.3	21.7
	Territorial	Jan.	88.3	11.7
	Territorial	July		
	Territorial	Apr.	75.7	24.3
	Territorial	Jun.	88.3	11.7
	Territorial	July	86.7	13.3
	Mean		84.0	16.0
<i>Selasphorus platycercus</i> , ♂ ³	Breeding territory	July	75.8	24.2
	Average for 3 spp.		81.6	18.4

¹ Stiles, 1971, including data of Pearson, 1954; ² Wolf and Hainsworth, 1971; ³ Waser and Calder, unpublished.

TABLE 5
Time-Energy Budgets of Hummingbirds.

Species	Approx. body size (g)	Status	Total kilojoules	Multiple of standard metabolic rate ^m
<i>Archilochus anna</i> , ♂	4	Feeding territory: Nocturnal homeothermy	43.18 ¹ , 29.82 ²	3.24
		Nocturnal torpor	31.59 ¹ , 22.25 ²	2.42
<i>Archilochus anna</i> , ♂	4.5	Breeding territory (Jan.): Nocturnal homeothermy	22.80 ³	2.48
		Nocturnal torpor	33.86 ²	3.68
<i>Archilochus anna</i> , ♂	4.5	Breeding territory (Mar.): Nocturnal homeothermy	23.84 ²	2.59
		Nocturnal torpor	28.28 ³	3.07
<i>Archilochus anna</i> , ♀	4.8	Incubating	37.30 ²	4.05
<i>Archilochus anna</i> , ♀	4.8	Incubating	28.47 ²	3.10
<i>Archilochus anna</i> , ♀	4.8	Brooding	22.35 ^{4,5} , 17.52 ^{4,6}	2.43(1.91)
			26.45 ^{7,5} , 20.04 ^{7,6}	2.88(2.18)
			30.91 ^{7,5} , 21.64 ^{7,6}	3.36, 3.22
			(29.60 ^{7,5} , 20.57 ^{7,6})	(2.35, 2.24)
<i>Stellula calliope</i> , ♀	3	Incubating	30.96 ⁸	5.27
		Incubating, night only	(7.74 ⁸)	
<i>Selasphorus flammula</i> , ♀	2.7	Incubating, night only	(12.55 ⁹)	
<i>Eulampis jugularis</i> ¹⁰ , ♂	9.9	Territorial	(10.02 for 325 min)	
<i>Eulampis jugularis</i> ¹⁰ , ♂	9.9	Territorial	(80.52 for 1889 min)	
<i>Eulampis jugularis</i> ¹⁰ , ♂	9.9	Territorial	(23.47 for 535 min)	

¹ Pearson, 1954; ² as recalculated by Calder, MSa, using Lasiewski's (1963a) metabolic data; ³ Stiles, 1971, values for daytime only, 10.65 and 12.52 hr, respectively; ⁴ data of Howell and Dawson, 1954; ⁵ assuming ¾ of absence in flight; ⁶ assume ¼ of absence in flight; ⁷ Calder, MS⁶; ⁸ Calder, 1971; ⁹ Hainsworth and Wolf, 1972c; ¹⁰ Wolf and Hainsworth, 1971; ¹¹ Lasiewski and Dawson, 1967.

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daily energy budget is 2 to 5 times that standard thermoneutral metabolic rate, and (2) there is no clear difference between the sexes in total energy requirements. It is also interesting that assuming a gram-specific energy content similar to eggs of the domestic fowl, each hummingbird egg represents perhaps 24 to 34% of the energy that the hen will later expend per day of incubating.

ENERGY CONSERVATION

We have seen that the duration of fasting which a bird can withstand is inversely related to body size (pp. 110-116, equations 44-50), and have considered the problem of nocturnal survival at the small end of the scale in bird sizes. Man responds to the threat of shortage by seeking to extract more. In nature, animals conserve. Hummingbirds could conserve energy reserves by careful choice of microhabitats and by reducing the metabolic rate through hypothermic torpor.

Hypothermic Torpor

When the body temperature is reduced, the gradient for heat loss from body to environment is less "steep," reducing heat flow and the metabolic requirement for heat production. As the tissues cool, the metabolic rate is decreased by the " Q_{10} effect." In hummingbirds a decrease of 10°C . may reduce the metabolism to one-fourth the previous value (Lasiewski, 1963a; Lasiewski and Lasiewski, 1967). The subject of hypothermic torpor has been reviewed recently, in detail (Dawson and Hudson, 1970; Calder and King, 1974).

The most important revelation in the understanding of torpor in hummingbirds of recent years has been that the hypothermic state is one of regulated homeothermy at a lower body temperature, 18 to 20°C in *Eulampis jugularis* and 10 to 12°C in *Panaterpe insignia* and *Eugenes fulgens* and 7°C in *Oreotrochilus estella* (Hainsworth and Wolf, 1970; Wolf and Hainsworth, 1972; Carpenter, 1972 and 1974) (see Figure 10). The nest temperature of *Selasphorus platycercus* reaches a low of 6.5 to 7°C during torpor, and further cooling appears to be prevented by regulation (Calder and Booser, 1973). During exposure to air temperature below the lower regulated body temperature of torpor in the species studied by Hainsworth and Wolf, oxygen consumption is increased in proportion to the temperature difference ($T_b - T_a$) and in parallel to the regression for normothermic metabolism below the lower critical temperature. This seems to put to rest the earlier misconception that torpor was a form of poikilothermy. A hypothetical scheme relating torpor to body size and other energetic factors in hummingbird evolution is seen in Figure 11.

Field Observations of Torpor or Hypothermia.—Most of the available information on torpor in hummingbirds has come from captive birds in the aviary and laboratory. As Lasiewski (1963a) and Dawson

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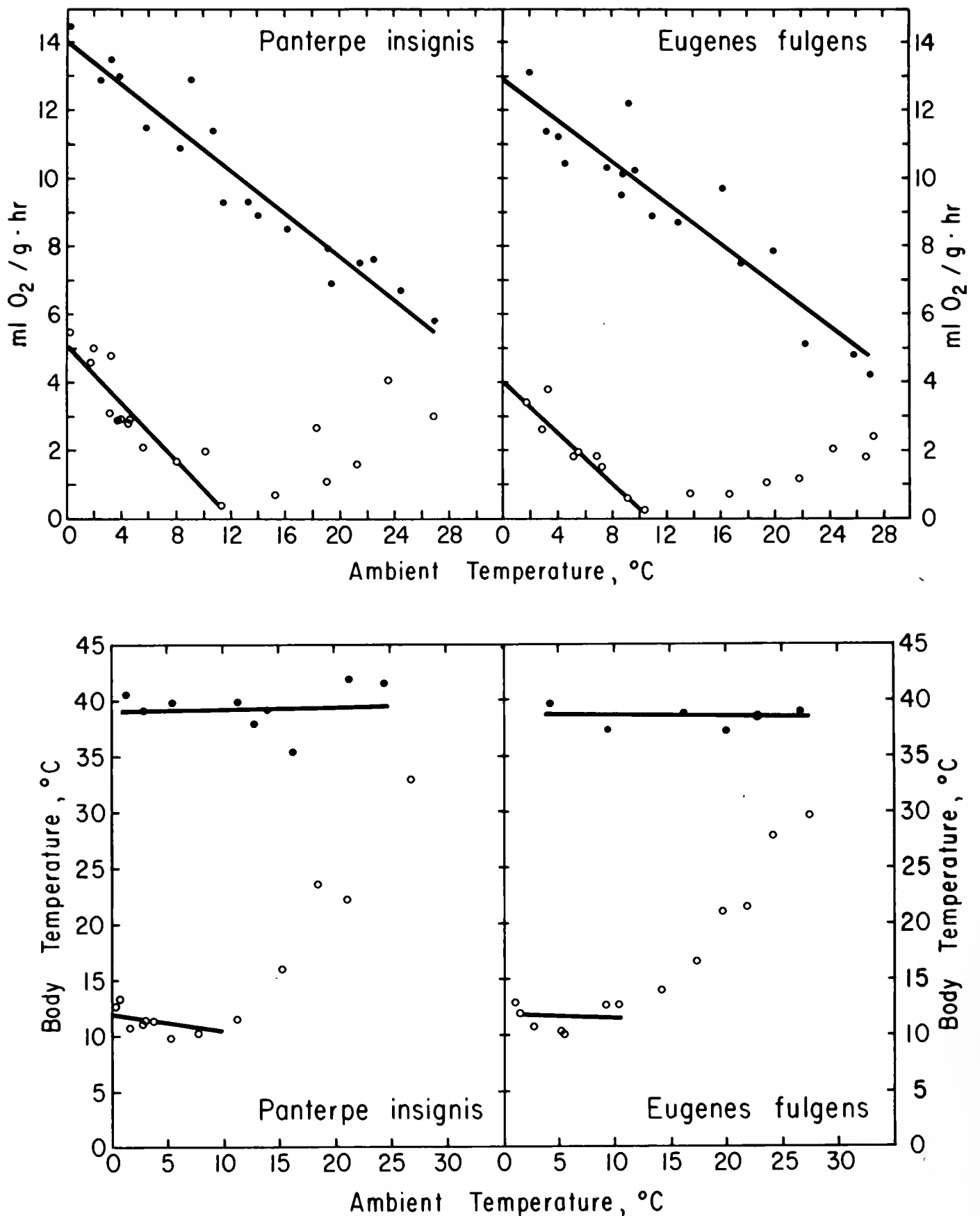


FIG. 10. Regulated torpor in two species of hummingbirds. Top: Metabolism as a function of environmental temperature. Bottom: Body Temperature as a function of environmental temperature. (From Wolf and Hainsworth, 1972.)

and Hudson (1970) have pointed out, hummingbirds can maintain nocturnal homeothermy with an adequate energy intake; conversely, torpor results from depletion of energy reserves. This makes the limited observations of torpor in nature of special interest with respect to questions of cause (climatic and feeding conditions), depth of hypothermia, and the timing of onset and arousal. These are summarized in Table 6.

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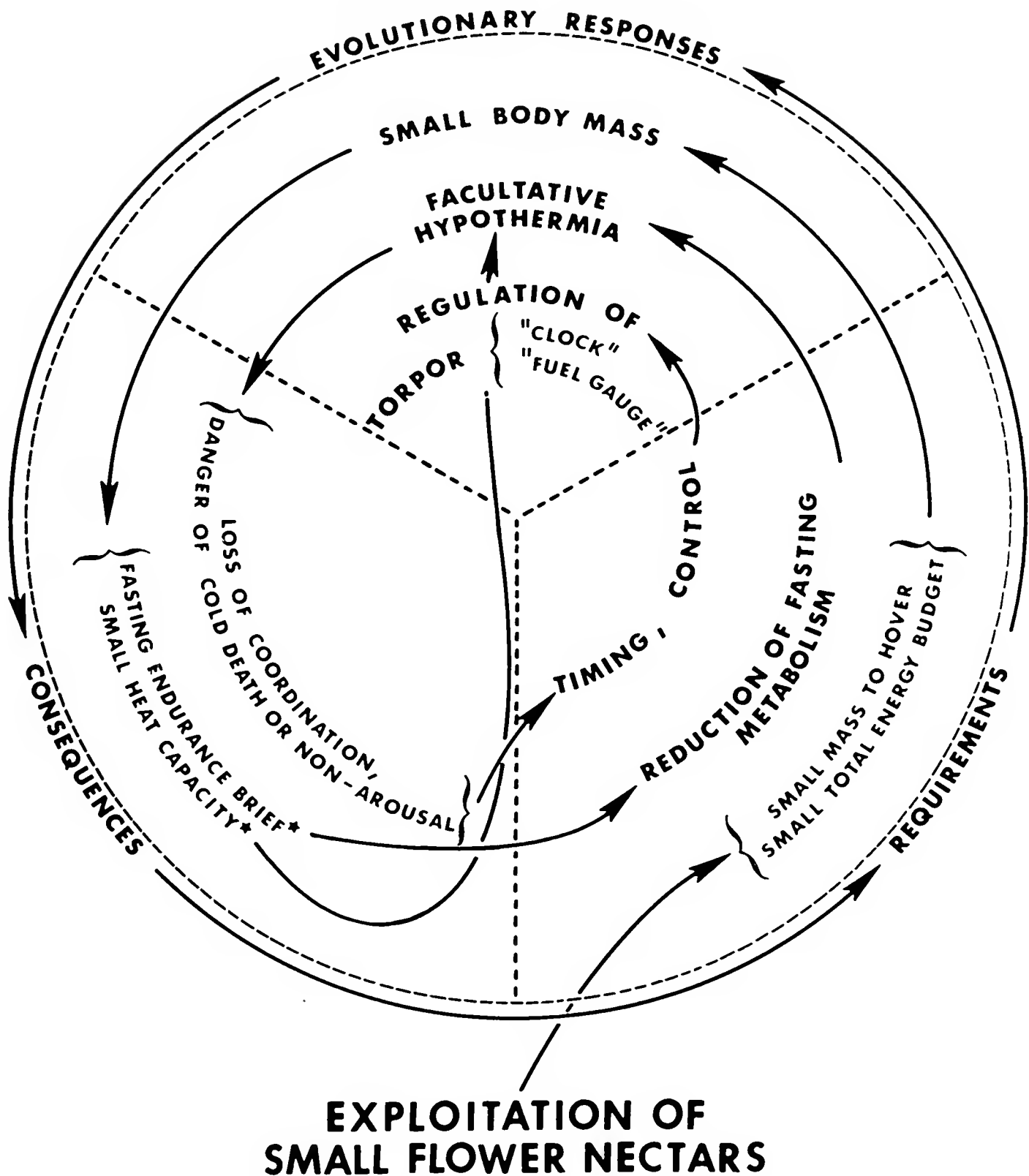


FIG. 11. A hypothetical scheme for some energetic aspects of hummingbird evolution.

Continuous recordings of nest temperatures for the Broad-tailed Hummingbird (*Selaphorus platycercus*) indicated, by lack of cooling intervals, that the females did not take feeding recesses during rain-showers in the day preceding episodes of nocturnal hypothermia (Figure 12). Neither rain during the non-feeding nighttime nor colder air temperatures resulted in hypothermia (Calder and Booser, 1973; Calder, *in press*).

Microhabitat

Endogenous thermoregulation may place demands on either the energy budget or the water economy, or both. While the availability

TABLE 6
Some Records of Natural Torpor in Hummingbirds.

Species	Time	Air temperature (°C.)	Minimum body temperature (°C.)	Conditions
<i>Archilochus alexandri</i> ¹	0200-0600	13	17	Advanced nestlings
<i>Archilochus anna</i> , ♀ ²	Daytime	Cold spell	--	Lawn, Oakland, California
<i>Archilochus anna</i> , ♂ ²	0300	15	"slightly warm"	Naked alder branch, 2.4 m above ground, 0.9 m from trunk
<i>Calypte costae</i> ¹	0400-0600	20	25	Advanced nestlings
<i>Oreotrochilus chimborazo</i> ³	2015	--	--	Cave, 4,340 m, Ecuador
<i>Oreotrochilus chimborazo</i> ³	2105	5	--	Cave, 4,340 m, Ecuador
<i>Oreotrochilus estella</i>	0030	14	14.5	In tunnel, Peru, above 3,800 m
<i>Oreotrochilus estella</i> ⁵	--	<7	7	Cave, Peruvian high plateau
<i>Selasphorus platycercus</i> ⁶	0100-0445	-1	6.5 ⁸	Nests under spruce boughs. Missed feedings during rainstorms preceeding day, 0830-0945, 1520-1710. Colorado, 2,900 m.
<i>Selasphorus platycercus</i> ⁷	0200-0430	1 to 8.5	(11 to 13.6) ⁸	Nests in aspen and spruce during nights following afternoon rains and missed feeding (4 nests, 7 instances of torpor including incubation, brooding, and post-brooding stages). Colorado, 2,900 m

¹ Lasiewski, unpub.; ² Pearson, 1950; ³ French and Hodges, 1959; ⁴ Pearson, 1953; ⁵ Carpenter, 1972; ⁶ Calder and Booser, 1973; ⁷ Calder, in press; ⁸ nest temperature minima.

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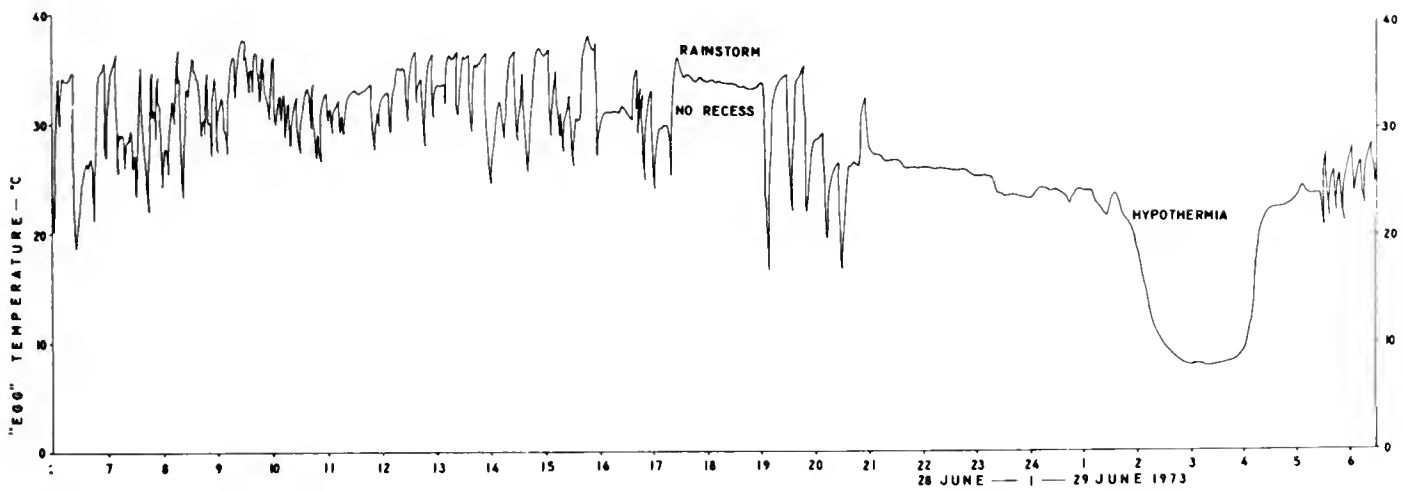


FIG. 12. A recording of temperature in the nest of a Broad-tailed Hummingbird, including an episode of fasting during a rainstorm which resulted in an energy shortage and nocturnal hypothermia.

of a food resource presents an opportunity in one sense, it may also attract a hummingbird to a thermally stressful macroenvironment. The cost of living there can be ameliorated through microhabitat selection of the best sites within the macroenvironment. Of course, the microhabitat must be selected with regard to other factors such as exposure to predators. However, there are some anecdotal but clearcut cases of behavioral selection for reduced exposure.

Before sunrise on cold mornings, the male Anna's and Broad-tailed Hummingbirds on their feeding/breeding territories perch low in the vegetation, where wind velocities are reduced and they are partially shielded from the radiative heat-sink of the cold sky, which is as cold as -20°C or colder in the Rocky Mountains. On hot days, the male Anna's and Costa's Hummingbirds spend the period of most intense solar radiation in shaded branches.

During the cold afternoon following passage of an early January cold front near Tucson, the territorial male Anna's Hummingbird's perch was a palo verde (*Cercidium microphyllum*) branch that was sunlit in the windbreak of a young Sahuaro (*Cereus giganteus*) column (Figs. 13, 14). I have already cited Swan's (1952) report of the daily retreat of hummingbirds from high elevations (4,420 m) to lower at the onset of cold fogs.

During the day hummingbirds are constantly replenishing their energy stores, and are active and generating waste heat. It is at night that the heat energy crises are more likely to occur. *Oreotrochilus estella* and *O. chimborazo* roost and nest in caves and crevices in the high Andes (Pearson, 1953; French and Hodges, 1959; Dorst, 1963).

The nests of female hummingbirds are easier to locate than the roosts of males and nonbreeding hummingbirds and are therefore useful for microhabitat studies. Dorst (1962, 1963) found that 70% of *Oreotrochilus estella* nests in rocks were facing east to take advantage of solar radiation in the early morning and to avoid an excessive solar load in the afternoon, but the majority of *O. chimborazo* nests studied by Smith (1969) were not oriented to the east because the cliffs did

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T_A 3.8°C
WNW
WIND
19 KM/HR



FIG. 13. The perch of a female Anna's Hummingbird in Tucson after passage of a cold front. Maximum air temperature 3.8°C, wind 49 to 63 cm sec⁻¹. The palo verde branch was directly downwind of the Sahuaro column which served as a wind break, while the bird was warmed by the sun. This perch was not used except during such weather, during which the bird was so reluctant to leave that it tolerated photography from 40 cm without flying.

not face east. Bent (1940), Wagner (1955), Dorst (1962) and Smith (1969) have all commented qualitatively on the thickness of nests of hummingbirds in cold climates. However, quantitative information on the insulative value of hummingbird nests has not yet been pub-



FIG. 14. The perch of a male Anna's Hummingbird during mid-afternoon on a hot day, shaded by palo verde branches which would reduce total heat load.

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lished, although Horvath (1964) has indicated that such might be forthcoming.

Horvath (1964) also observed that Rufous Hummingbirds (*Selasphorus rufus*) nest low in conifers in spring but higher in deciduous trees in the summer. He pointed out that in the spring, the deciduous trees had not leafed out and thus did not provide an effective screen for radiative exchanges.

Hummingbird nests are often protected by an overhang or overhead branch (Bent, 1940; Wagner, 1955; Dorst, 1962; Smith, 1969; Calder, 1971, 1973a). The protection may be from precipitation and predation (Bent, 1940), "hail, rain, and the midday sun" (Smith, 1969) and(or) nocturnal radiative loss (Calder, 1971, 1973a). I have measured the total hemispherical, long-wave radiation influx at nests of the Broad-tailed Hummingbird and the surface temperatures of incubating and brooding hens during the coldest presunrise hour at 2,900-3,000 m elevation in the Colorado Elk Mountains (Fig. 15). The net radiative loss is equivalent to 13.5% of the total metabolic power of a hummingbird exposed to a similar air temperature (5°C) in the laboratory (from Lasiewski, 1963a). If the nest were exposed to the open sky (-20°C) hemispherical influx (no shielding branches) instead, the net radiative loss might be equivalent to 29.3% of the laboratory metabolic rate (nontorpid) at 5°C (Calder, *in press*). Thus overhead shelter can cut radiative losses in half.

Similar in effect to overhangs and branches, vertical relief in local topography and surrounding trees can obstruct the "view" of the cold sky, so that radiative exchange is with sun-warmed rocks and tree trunks. An Anna's Hummingbird which nested in February near Tucson incubated when air temperature descended below freezing. The nest was located in a cottonwood tree (*Populus fremontii*) near the mouth of a canyon, where the canyon walls blocked 29.6% of the celestial hemisphere. The nest was placed beneath a branch, which with surrounding trees blocked out an estimated 26% more of the sky, resulting in a reduced net radiative heat loss (Calder, 1974a).

Thus to fully understand the problems and advantages of a particular perch, roost, or nest site, it is necessary for us to consider all aspects of the microenvironment: radiation, convection, conduction, and evaporation. With the limited fasting endurance inherent in small body size, hummingbirds can be expected to make especially careful use of vegetation, topography, orientation, and airflow patterns in order to conserve heat and energy reserves.

With an awareness of the implications of body size for avian energetics and of the physical principles of heat exchange, new insight into the behavior and the natural history of birds can be possible. At the small limits of body size, hummingbirds have both the ability and the necessity to fit into the optimal microclimates of a given macroclimate.

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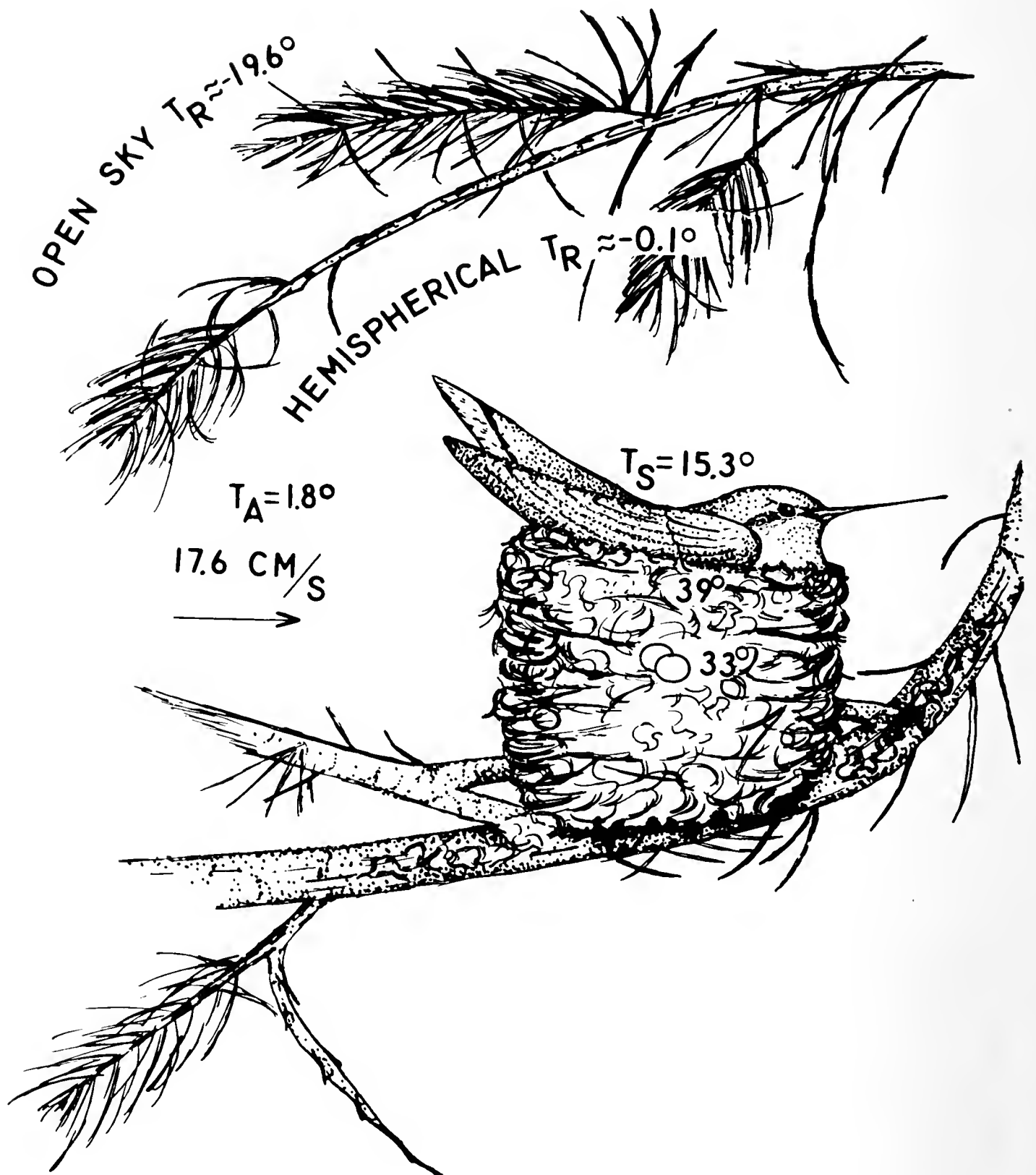


FIG. 15. Factors in the heat exchange of a Broad-tailed Hummingbird, incubating in the pre-dawn chill of a high valley in the Colorado Rockies. (From Calder, *in press*.)

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DISCUSSION

WILLIAM R. DAWSON: I would like to congratulate Dr. Calder. I discovered as a young Ph.D. that not everyone shared my enthusiasm for exponential equations as an art form. He has made them most palatable, and this is quite an accomplishment. I would also like to thank him, as one who was close to Bob Lasiewski, for his extreme graciousness in acknowledging the significant contributions Lasiewski made in his lifetime to some of the problems Calder's considered.

We are in a position here to comment on several things and I will lead off, since this is an area in which I have had considerable interest. First of all, Bergmann's rule, of course, is something of which people

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who work in avian or mammalian systematics are aware. It seems to me that Calder's comments call attention to the fact that a simplistic explanation of this cannot be valid. As Ernst Mayr pointed out in his classic controversy about 18 years ago with Scholander, the measurements supporting this rule are certainly real. Physiologists have probably erred in interpreting this rule primarily in terms of surface-volume relations. What the geographic trends in size within given kinds of birds may represent, judging from Calder's and King's presentations, are optimizations with reference to a variety of considerations, not just that relating to heat conservation.

What might a species of bird conforming to Bergmann's rule achieve? The larger representatives of it occupying cooler climates will have a heavier burden of acquiring resources, owing to their greater size. What might they gain? The thing that was mentioned was greater survival time while fasting. As a displaced Californian, who has been trying to come to terms with the Michigan climate for 20 years, I am all too aware of the fact that it's not the usual winter day that sorely challenges birds, it is those terrible intervals involving ice storms and other forms of inclement weather that interrupt the acquisition of food resources. Relatively large capacities for surviving without food might be critical in such intervals.

But in addition to this, I should amplify the point that some indication exists that being heavier allows one to protect oneself better in terms of the amount of insulation that one can carry. This is a particularly important thing for birds, because as Laurence Irving has pointed out, the feathers obviously serve two basic but not necessarily congruent functions. One of these is obviously flight, and the other one is insulation. In this particular case, I think that perhaps being able to carry a little more insulation and still locomote effectively might have some advantages.

There are some more aspects to this, but I would simply reiterate—and ask Calder to comment in a moment—that probably what we see in the size clines is something conforming to Bergmann's rule, for which a single geometrical explanation will not suffice. What we are possibly seeing are the consequences of a series of optimizations. Biological phenomena are typically complex, and we obviously run risks in attempting to explain many of them in terms of single considerations that are satisfying to us, but in retrospect are insufficiently all-embracing.

DR. CALDER: It is obviously undeniable that these trends in body size exist. It is also undeniable that as the bird gets bigger his cost per gram is cheaper. However, it isn't cheaper for the whole bird and the total cost of thermoregulation does not explain the trend. An energetics explanation such as fasting endurance might explain it, and obviously there are other factors we haven't stumbled on. Brian

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McNab's (1971) point is that the simple "per gram body weight" basis is incorrect for considering the problems of the whole bird.

DR. DAWSON: Another comment I'd like to make on Calder's presentation concerns the "New Trochidology" as it's referred to in his manuscript. The particular thing that I was wondering about was the effect of the female hummingbird's becoming torpid while incubating on the duration of the incubation period. Thomas R. Howell and I studied attentiveness by an Anna Hummingbird some years ago, shortly after Oliver Pearson had documented the occurrence of torpor in this species. We wondered whether torpor would occur in the female we were studying. We were particularly interested in this since hypothermia in the hen and consequent cooling of the eggs might significantly prolong the incubation period. Our Anna Hummingbird, of course, did not become torpid. Subsequently, Lasiewski and you did find torpor in certain incubating hummingbirds of other species. Did this substantially prolong the incubation period, and if it didn't, is there any suggestion of some compensatory mechanism that we haven't as yet identified?

DR. CALDER: Our records are for a maximum torpor cycle duration of about four hours; this is four hours of a sixteen to nineteen day incubation period. That amount wouldn't be enough to show up, although it must slow development, if only briefly.

DR. DAWSON: This would be one perhaps per night?

DR. CALDER: If they had to do it every night it was a poorly planned nest or feeding was marginal and it should retard development perceptibly.

DR. DAWSON: The other comment I have, which also relates to hummingbirds, I like hummingbirds, is that your record of nest temperatures indicates a minimum of 10°C. There's a great deal of ambiguity, as far as torpor in birds is concerned, concerning the thermal limit for spontaneous arousal. We have on the one hand a whole body of literature on southern California birds, principally ones that have been studied by Bartholomew and associates, in which there's good indication for not only hummingbirds but others like Caprimulgids, that 12-15°C seems to be a lower limit for spontaneous arousal. Some other work contains indications of much lower thresholds for arousal. For example there's *Oreotrochilus* roosting in the caves of the high Andes. It becomes torpid at night at temperatures as low as 3 to 5°C. David Ligon had a poor-will, not from southern California, but from Idaho, which was apparently regularly going into torpor, existing at a body temperature of 6°C, and then spontaneously arousing. My

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question is, do you think that the value of 10°C you observed is indicative of body temperature of the incubating hummingbirds, and, if so, are we going to have to modify our ideas of the lower temperatures at which these animals can spontaneously arouse?

DR. CALDER: As discussed in my manuscript, I think that Reed Hainsworth and Larry Wolf (Hainsworth and Wolf, 1970; Wolf and Hainsworth, 1972) have done the latest and most significant work regarding temperature regulation and torpor. Their work shows that torpor is not a passive conformity wherein the hummingbird becomes a temporary poikilotherm. The "thermostat" has just been set to a lower point, where parallel to the normothermic metabolic curve, its metabolism is regulated proportional to the thermal gradient [$\dot{H}_m = h(T_b - T_a)$]. The lower body temperature for *Eulampis* was around 20°C, and for two other species it was 12-14°C. The temperatures I recorded were just somewhere between the bird and the outside world, and since it's a fake egg, I don't know what the hen's minimum care temperature was, actually.

DR. DAWSON: One of the things that people who have worked in the area of avian and mammalian physiology have been most intrigued with is the fact that there seem to be indications of some sort of a magic lower limit in size that lies somewhere in the vicinity of 2 grams. We know that some of the early explanations of this limit are too simple. Interestingly it seems as though some new insights into these energetic problems, which I think have been very eloquently portrayed for you by Calder, are actually coming from, of all things, the study of some of the larger insects, which require high temperatures for flight. In a burst of ecumenicism I should like to ask Dr. Bartholomew, who has done some work in this field, and has students who have worked in this area, to make some general comments concerning the stance that these insects have in relation to high temperatures, because, you see, they range in size from smaller than the smallest homeotherms up to perhaps 10 grams. Perhaps some perspectives can be gained here from information on the energetics of these insects.

GEORGE A. BARTHOLOMEW: Five years ago I had a graduate student named Bernd Heinrich. Every time he went out in the desert with mist nets to look for birds, he came back with butterflies, and he convinced me, reluctantly and painfully, that it was not only perfectly reasonable, but desirable, to consider butterflies and moths and hummingbirds as examples of convergent evolution. On the basis of his strength of personality, I reincarnated as an insect physiologist, turned in my mist nets for butterfly nets, went to the tropics, and began to study big moths. As you know, moths overlap the smaller birds in size, some of them weighing as much as 8 or 10 grams. The remarkable

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thing is that these giant moths cannot fly unless their body temperature reaches 35-40°C. Moreover, these high body temperatures are produced by heat endogenously generated by quivering the wing muscles—a process analogous to shivering in birds and mammals. Thus we are forced to treat these large moths as endothermic, warm-blooded animals. The same may be true of most heavy-bodied insects, and certainly it applies to most of the heavy-bodied forms within the Lepidoptera. The striking thing is, however, that many of these “warm-blooded” insects have a body weight that is much much less than the 2-gram minimum which exists among birds, the smallest being some of the bee hummingbirds of the Antilles. Indeed, I have measured moths weighing only 75 milligrams, which can, in about 15 seconds, raise their thoracic temperature from 20°C to 38°C by quivering their wings. Only when they get up to operating temperature, do they fly away. There is an evolutionary message here, I think. Moths face exactly the same ecological problems as hummingbirds; they are hoverers and they feed on small amounts of nectar in flowers. The striking thing is that moths and hummingbirds have evolved strategies that are similar but are mirror images. Moths are ectotherms most of the time, becoming endothermic only during activity. Consequently, they need not squander any of their limited energy resources on temperature maintenance except during the act of flying. The result is that moths may be perfectly good endotherms for 20 minutes of the day, and ectotherms for the rest of the time. As a result they face the acute energetics problems resulting from small size and endothermy for a much smaller fraction of the time than is the case with hummingbirds. So, we can say that moths have evolved essentially the same strategy as hummingbirds but with a drastic shift in the relative time spans of ectothermy and endothermy in their daily cycles.

DR. DAWSON: I'd now like to call on Dr. Kendeigh, who's worked in this area of allometric relations and, as you recall, did some work cited by Dr. Calder. I think he has some brief comments.

S. CHARLES KENDEIGH¹: It is fine to see Dr. Calder attempt to quantify and correlate body organ masses and functions and activities of various sorts with size (weight) of the bird. Once such relationships can be firmly established for a few species, we will then be able to predict how any of the 8,656 species in the world are made, function, and behave and how these are correlated with the amount of energy required and the environmental resources available. But some caution is required.

Regression equations.—Lumping data from a variety of species to obtain regression lines and equations of metabolism on temperature presupposes that acclimatization or physiological adaptation to differ-

¹ For the convenience of the reader, Dr. Kendeigh has elaborated upon his oral presentation and also included references to pertinent literature.—Ed.

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ences in local climates does not affect metabolic rate. Scholander, back in 1950, compared arctic with tropical birds and mammals, and contended that adaptation to climate involved changes in insulation affecting heat production. His conclusion, generally accepted for the last 20 some years, that metabolic rate is related to body weight regardless of differences in local climate, is being called into question.

Hudson and Kimzey (1966) showed that basal and standard metabolism of house sparrows from northern states is higher than in birds from Texas. Trost (1972) demonstrated that Horned Larks, *Eremophila alpestris*, in a hot desert environment have lower rates of metabolism than subspecies in milder climates. Just recently, Dawson and Bennett (1973) have shown the same thing for pigeons and doves. Dr. Charles Blem and I have further information on this problem.

Dr. Blem measured existence metabolism of collected samples of live house sparrow, *Passer domesticus*, obtained both in midwinter and midsummer, from eight localities scattered from Florida, Texas, and Arizona to Churchill in northern Manitoba (Blem, 1973). When these measured rates at mean winter and summer temperatures are compared with rates predicted from equations obtained on birds in central Illinois, it is immediately obvious that birds from northern localities tend to have rates higher than predicted and those from southern localities have rates lower than predicted. Most measurements of metabolic rates have been done with birds from temperate climates and hence the regression lines usually compiled apply strictly only to birds with this adaptation. Allowances need to be made when applying the equations to birds from colder or warmer climates (Kendeigh and Blem, 1974).

Summit metabolism.—Calder makes a comparison of energetics of flight and summit metabolism and attempts to predict summit metabolism from a regression equation based on weight. Here again we run into the complicating factor of physiological adaptation to local climate. I pointed this out in my paper on tolerance to cold and Bergmann's rule (Kendeigh, 1969). In terms of per gram metabolic weight ($W^{0.53}$), for instance, the summit existence metabolism of tropical species is about 4.9 kcal/day, while for temperate and arctic species it varies from 5.3 to 6.9 kcal/day. A 19-gram Tree Sparrow, *Spizella arborea*, nesting in northern Canada, has a higher summit metabolism than a 37-gram Green-backed Sparrow, *Arremonops conirostris*, resident in the tropics. Weight certainly is of importance but one cannot obtain a close prediction of summit metabolism using weight alone.

We must not also forget that there is seasonal acclimatization in rates of metabolism in many species, including summit metabolism. Barnett (1970) found in the House Sparrow, for instance, that the birds in mid-winter will tolerate ambient temperatures down at least to -25°C , which requires a maximum expenditure of existence metabolism of nearly 33 kcal/bird-day while in late summer they tolerate only about 0°C and can mobilize only about 25 kcal/bird-day.

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Bergmann's rule.—Coming back to Bergmann's rule, Calder's suggestion that a larger size permits greater energy storage on the body which with relatively lower rates of metabolism gives greater survival capacity for periods when food is not available, as at night or in times of stress, is interesting. Certainly it should be included as one of the advantages of larger size, although not necessarily the most important one.

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DR. CALDER: I certainly concur with Dr. Kendeigh's note of caution concerning predictions from the allometric equations. Certainly individual adaptations are lost in this lumping procedure. Hudson and Kimzey (1966) found that standard metabolism of House Sparrows from Syracuse was 26% higher in thermoneutrality and 40% higher at 0°C than that of House Sparrows from Houston.

Hence I must emphasize that the allometric equation is useful only (1) for showing the effect of body size all other things being equal (and we know they probably are not), (2) for giving a general baseline against which specialists for extreme environments can be compared, and (3) as a ballpark estimate for identification of significant problems and designing experiments.

If pursued further, we might encounter the same basis for refinement that has been found in metabolic equations. First of all, birds and mammals should be analyzed separately, then passerines and non-passerines were separated, and then day (α) and night (ρ) and so forth. However, if we go to narrowing the group down too much taxonomically, we wind up within a family where you don't get too much size range so that you get a buckshot pattern.

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I also agree with Dr. Kendeigh in regard to Bergmann's Rule. The relationship between size and fasting endurance is only one possibility that came to mind, and certainly others should be sought, as the morphological trends are exceptionally well documented. My main point was just to emphasize what McNab (1971) said, that arguments cannot be based on energetic economy per gram body mass, because the bigger the bird, the more he must eat!

DR. DAWSON: Finally, as far as the discussants are concerned, Dr. Odum would like to have a brief word or two.

DR. EUGENE P. ODUM: Dr. Calder has shown you the best of both of the worlds, that is, the levels of organization that we were discussing earlier. He first presented very elegant models for looking at the problem with a "macroscope", as it were. Such models are excellent for making first order predictions. If the predictions turn out to be good, then following the parsimonious principle one may not need to go further. If prediction is way off the mark, then reexamination of parameters is in order. For example, somebody comes up to you, and says, "Hey, what's the size of the territory of the blue-feathered sparrow?", something that perhaps nobody has measured. With a good model for territory size in sparrows one could whip out a little pocket calculator and come up with an estimate. For many purposes this would be good enough, but if one really needs to know, or if one wishes to test the model it may be worthwhile to go out and measure it (or put a student on it).

The other important thing Dr. Calder did was to show you the proper use of micro-environmental data. His model first showed that for hummingbirds heat loss by radiation at night was a critical factor. This not only suggested a reason for the observed fact that the species in question nests under a protecting overhead shelf or limb, but it pointed directly to what microclimatic factor was operationally significant and where it should be measured. Contrast this with the non-selective approach of measuring 150 different things, more or less at random, and then wondering what to do with all the data!

ENERGETICS OF REPRODUCTION IN BIRDS

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INTRODUCTION

Reproduction has been a major focussing point in studies of avian physiology, behavior, ecology, and evolution. The fascination of the reproductive process has drawn the attention of ornithologists for generations; the reproductive behavior of birds has also been an arguing point for a major evolutionary controversy over the adaptive significance of population recruitment rates (e.g., Wynne-Edwards, 1962; Lack, 1954, 1966). But the intensity of this controversy, which has grown pale from the loss of vitality that every argument suffers with time, has obscured some basic and much neglected aspects of reproductive biology, including the energetics of reproduction.

Ornithologists have investigated energetic aspects of reproduction since the early work of Pembrey (1895) on the development of temperature regulation, of Tangl (1903) on the energy content of eggs and efficiency of embryonic development, and of Kendeigh (1934, 1963) on the relationship of energetics to the environment. But in spite of a rapid accumulation of information on the energetics of reproduction, no major synthesis of the topic has appeared and, in particular, we have only a rudimentary understanding of the role that energy utilization plays in the evolution of the reproductive strategy.

My purpose in this paper is not to provide a synthesis; our knowledge and understanding of reproductive energetics are still below the threshold for that major step. Instead, I have tried (a) to summarize major patterns of energy use during the reproductive cycle, (b) to provide a framework for organizing information on reproductive energetics, (c) to suggest directions for future study, and (d) to indicate some of the relationships that must eventually be incorporated into any synthetic view of reproduction.

Several aspects of reproductive energetics have been reviewed recently. King (1973) discussed energy requirements for gonadal growth, egg production, and incubation; Drent (1970) reviewed literature on the energetics of incubation in conjunction with his own detailed studies on the Herring Gull (*Larus argentatus*); King and Farner (1961) reviewed the development of thermoregulation in their summary of avian energetics; Brody's (1945) classic treatise on the ener-

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getics of production in domestic animals remains a standard reference to this day.

This review enlarges upon previous works in its scope and organization. I have tried to consider all aspects of energy utilization during the nesting cycle. I have further endeavored to point out energetic relationships between adaptations of different parts of the nesting cycle and between the adaptations of adults and their young. Because my own bias is decidedly evolutionary, much of the information on energetics compiled here bears on the adaptive significance of reproductive behavior patterns. The review concentrates on strategies of energy utilization by parents and offspring. Problems of energy procurement are not considered. Thus I have deliberately avoided the question of clutch size determination; I have found little in this study to add to previous reviews of this problem (see Klomp, 1970; Cody 1966; Lack, 1947, 1954, 1966, 1968; Hussell, 1972). The adaptive significance of clutch size is too closely tied to demography (Williams, 1966; Gadgil and Bossert, 1970) and resource procurement (see Ricklefs, 1970) to be considered here. I have also ignored the energetics of behavioral aspects of reproduction, such as territorial defense, courtship, and nest building, that are not directly related to the production of the young.

The review begins with a summary of the energetic equivalents of gas exchange and body tissue. Adult metabolism is then described to provide a standard of comparison for energy requirements of reproductive processes. The energetics of stages of the reproductive cycle are taken up in temporal sequence: gonadal growth and egg production, incubation, growth and development of thermoregulation, and adult energy expenditure for foraging.

ENERGETIC EQUIVALENTS

HEAT ENERGY CONTENT OF FOODS

During photosynthesis, green plants assimilate 9.33 kcal of energy for every gram of carbon fixed (Rabinowich and Govindjee, 1969). The various biochemical rearrangements of organic compounds that occur in the living body alter this value so that each type of organic compound has a unique and characteristic equivalent heat of combustion, which measures its potential release of energy in metabolism (Table 1). The most commonly accepted energetic equivalents for the major classes of organic compounds are carbohydrates (starch and glycogen) 4.1 kcal/g, protein 5.65 kcal/g, and fat 9.45 kcal/g (Brody, 1945). Kleiber (1961) suggests the slightly higher rounded values of 4.2, 5.7, and 9.5 kcals/g, respectively, which are followed by King and Farner (1961).

Most forms of life, including birds, are not capable of fully releasing the energy of proteins because they must rid their bodies of nitrogen in some organic form(s). In birds the excretion of nitrogen is often

TABLE 1
Chemical Characteristics and Combustible Energy of Some Important Organic Substances (based on Brody, 1945).

Compound	Chemical formula	Percent composition by weight				Heat content ¹		
		C	H	O	N	kcal/g	kcal/gC	kcal/gN
Starch and glycogen	(C ₆ H ₁₀ O ₅) _n	44	6	49	—	4.14	9.3	—
Glucose	C ₆ H ₁₂ O ₆	40	7	49	—	3.73	9.3	—
“Fat”	various	75	12	13	—	9.45	12.6	—
“Protein”	various	52	7	23	16	5.65	10.9	35.3
Uric acid	C ₅ H ₄ O ₃ N ₄	36	2	29	33	2.74	7.6	8.2
Urea	(NH ₂) ₂ CO	20	7	27	47	2.53	12.6	4.4

¹ g = gram; gC = gram of carbon; gN = gram of nitrogen.

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claimed to be primarily in the form of uric acid (heat equivalent 2.74 kcal/g, or 8.22 kcal/gN). Folk (1969) presents strong evidence that the detection of uric acid in avian urine results from an artifact of chemical analytic procedures. Nevertheless, even if excreted nitrogenous compounds are transformed to uric acid during urine analysis, the uric acid content of excreta still provides a useful index to nitrogen metabolism and urinary energy loss. Since 0.16 g of nitrogen must be excreted for every gram of nitrogen metabolized, 1.31 kcal (0.16 times 8.22) are lost in the urine, leaving the net metabolizable energy of protein as 4.34 kcal/g (5.65 minus 1.31).

Urinary nitrogen occurs not only as uric acid, however. Coulson and Hughes (1930) determined that 75% of the nitrogen in urine is excreted as uric acid, the rest is more or less equally distributed between urea, ammonia, creatinine, and allantoin. King (1957) calculated that this mixture of compounds has a caloric value of 8.10 kcal/gN; the low energy content per gram of nitrogen of urea, ammonia, and allantoin (5.4, 6.7, and 7.3 kcal/gN) was balanced by creatinine's rather higher value (13.4 kcal/gN).

Duck and chicken urine have average heat contents, determined by direct calorimetry, of 8.5 and 8.3 kcal/gN (Szalagyi and Kriwuscha, 1914: cited by King, 1957). These values exceed calculations based on the nitrogenous compounds in urine because small quantities of fats and other non-nitrogenous compounds are also excreted (0.018 g/gN in chicken urine). Using an approximate value of 8.3-8.5 kcals/g urinary nitrogen, we obtain 4.3 kcal/g for the metabolizable energy in protein. King (1957) obtained a slightly lower value (4.2 kcal/g) because of an error in subtraction.

Proportions of proteins, fats, and carbohydrates in foods vary widely depending on type (Table 2). All animal tissues are characterized by high protein content. The percentage of protein in grains, based on fresh weight, is deceptively high because grains contain relatively little water. Fruits of tropical and temperate species of plants add little protein to a diet. High fat contents characterize the flesh of some vertebrates, including fish, and some tropical fruits (oil palm and *Persea*). Shellfish, at least commercial varieties, have relatively little fat.

Because growth and reproduction require abundant sources of protein, the ratio of protein content (grams) to metabolizable energy (kcal) provides a useful index to the nutritional value of foods (the protein index). For convenience, I have multiplied these ratios by 100 (Table 2). Pure protein has a protein index of 23.3 ($100 \times 1 \text{ g protein} / 4.3 \text{ kcal metabolizable energy}$). As one would expect, animal foods have uniformly high protein indices (15 to 22), while those of fruits and grains are low.

The suitability of different foods depends on the particular demands of the organism. Protein and energy requirements of various reproductive processes, particularly egg formation, chick growth, and molt, will be discussed separately under each topic. One should also remember

TABLE 2
Nutritional Characteristics of Various Foodstuffs.¹

Food ²	Metabolizable energy (kcal/g) ³		Percentage composition based on wet weight				Protein index ⁴
	Wet weight	Dry weight	Water	Protein	Fat	Carbohydrate	Ash
Fruits							
(av. of 10 tropical species)	1.28	5.19	75.4±17.5 ⁵	1.4 ±0.6 ⁵	7.5 ±18.2 ^{5,6}	12.3 ±5.3 ⁵	—
(5 temperate species)	0.64	4.21	84.9 ±3.3	1.02±0.2	0.48±0.27	13.2 ±2.1	0.38±0.13
Grains							
(5 species)	3.72	4.22	11.8 ±0.8	10.9 ±2.4	2.4 ±0.7	73.2 ±2.9	1.7 ±0.6
Insects							
(5 species)	1.18	3.59	67.2±10.8	17.7 ±8.6	3.4 ±1.5	2.3 ±2.1	—
Marine invertebrates							
(7 species)	0.87	4.25	79.5±1.4	16.5 ±1.0	1.13±0.63	1.33±1.12	1.42±0.81
Fish							
(5 species)	1.42	5.29	73.1±4.0	19.4 ±1.7	6.2 ±3.8	0.0	1.60±0.60
Reptiles and amphibians							
(2 species)	0.82	4.12	80.2±2.4	18.1 ±2.4	0.4 ±0.1	0.0	1.15±0.07
Birds and mammals							
(5 species)	1.52	5.01	69.6±2.6	22.9 ±1.8	5.7 ±0.8	0.0	1.26±0.22

¹Tropical fruits and insects summarized by Morton (1973); remaining data from Watt and Merrill (1963).
²Edible portions only.
³Assuming 100% digestibility, protein = 4.30 kcal/g, fat = 9.45 kcal/g, and carbohydrate = 4.14 kcal/g.
⁴Percent protein content divided by metabolizable energy.
⁵Standard deviation (SD).
⁶Only the oil palm (58.4% fat) and *Persea* (11.3% fat) differ significantly from temperate fruits.

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that the foods listed in Table 2 are assumed to be 100% digestible. Most of the values do not include easily separated, undigestible refuse (feathers, bone, exoskeleton, hair, etc.), but even edible portions are not fully digestible. Efficiency of assimilation varies with the organism, the nature of the food, and with many ecological conditions that directly or indirectly influence digestive processes. These considerations should not greatly alter our overall evaluation of the nutritional quality of foods, however.

ENERGETIC EQUIVALENTS OF RESPIRATORY GAS EXCHANGE

Metabolic oxidation of organic compounds requires oxygen, and releases carbon from the body in the form of carbon dioxide and hydrogen in the form of water. The ratio, by volume, of carbon dioxide released to oxygen consumed (the respiratory quotient, or R.Q.) depends on the chemical composition of the material oxidized. For carbohydrates the respiratory quotient is 1.00, and for fats it is 0.71, assuming the chemical composition of fat given in Table 1 (King and Farner, 1961; Kleiber, 1961). The oxidation of fat requires relatively more oxygen compared to carbon dioxide liberated (lower R.Q.) than carbohydrates, because fat compounds contain less chemically bound oxygen than carbohydrates (Table 1).

Proteins have a lower respiratory quotient when oxidized than carbohydrates, both because of the lower oxygen content of proteins, and because oxygen is required for the formation of nitrogenous excretory products in urine. The respiratory quotient of protein varies, however, with differing nitrogenous waste products excreted in the urine. If uric acid is excreted, the R.Q. of nitrogen oxidation is 0.70, and if urea is excreted, it is 0.83. King and Farner (1961) adopted a value of 0.73 which is probably the best estimate for birds.

The energetic equivalent of oxygen consumption when carbohydrates and fats are metabolized is expressed by the equation

$$\text{kcal/l O}_2 = 3.82 + 1.23 \text{ R.Q.}$$

(King and Farner, 1961). Thus, the energetic equivalent of a pure diet of carbohydrate is $3.82 + (1.23 \times 1.0) = 5.05$ kcal/l O₂ and of fat it is $3.82 + (1.23 \times 0.71) = 4.69$ kcal/l O₂.

The energetic equivalent of oxygen consumption can also be calculated for a mixed diet containing protein if the gas exchange is corrected for protein metabolism. The excretion of one gram of urinary nitrogen is equivalent to 26.6 kcal of metabolizable energy, requires the consumption of 5.59 l O₂, and results in the production of 4.11 l CO₂ (King and Farner, 1961). Romijn and Lokhorst (1961) used a modified equation for calculating the thermal equivalent of gas exchange

$$\text{kcal} = 3.87 \text{ O}_2 + 1.19 \text{ CO}_2 - 0.30 \text{ N}$$

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where O_2 and CO_2 are liters and N is grams of urinary nitrogen. In practice, however, the error introduced by ignoring nitrogen in such calculations is small (less than 1%) compared to errors involved in measuring gas exchange. The energetic equivalent of oxygen consumption for the metabolism of pure protein is 4.75 kcal/l O_2 (26.6 kcals/gN divided by 5.59 l O_2 /gN).

COMBUSTIBLE ENERGY OF BIRDS

In his review of methods of direct calorimetry, Paine (1971:147) states that "for those individuals with the equipment, expertise, and time available, little accuracy will be lost by calculating caloric equivalents from chemical data." The composition of organisms and foods is more useful information than their caloric content alone, so I would recommend that chemical analyses should be made rather than, or in addition to, calorimetric analyses whenever possible.

Most analyses of body composition involve separation of the major chemical constituents: water, fat, ash-free lean dry matter (assumed to be mostly protein in birds), and ash. Processing methods vary considerably among authors (Rogers and Odum, 1964; Odum, Marshall, and Marples, 1965; Yarbough and Johnston, 1965; Kale, 1965; Ricklefs, 1967; Brisbin, 1968; Johnston, 1970). There is no general consensus for a single best technique and various modifications have been suggested to deal with species of differing body size and composition. Drying is usually best done under a vacuum at fairly low temperatures (40-60°C) to avoid driving off volatile lipid fractions. For example, Kale (1965) obtained average values of 6.17 and 6.60 kcal/g ash-free dry weight for adult Long-billed Marsh Wrens (*Telmatodytes palustris*) dried at 100°C in air and at 40°C in a vacuum, respectively. Kale's figures suggest that about half of the fat in the body had been lost at the higher temperature.

Fat solvents are used either heated or at room temperature, and have consisted of ethyl ether, methanol, ethanol, petroleum ether, or some combination of these, often including chloroform. Most extraction procedures are intended to remove fats used primarily for energy storage (triglycerides) and structural fats (phospholipids). Some authors separate these components (see, for example, Yarbough and Johnston, 1965, and Lawrence and Schrieber, 1974). Ash content is usually determined by combustion in a muffle furnace at 550-600°C. But Paine (1971) has suggested that temperatures above 500°C may cause the loss of some calcium carbonate from the ash residue.

The energy equivalent of extracted fats is never as great as the expected value of 9.45 kcal/g, partly because the caloric value of phospholipid is lower than that of pure triglyceride fats and partly because other impurities are often extracted by fat solvents. Odum, Marshall, and Marples (1965) obtained an average of 8.94 ± 0.05 (SE) kcals/g upon the combustion of extracted fat from small passerine birds. The energy content on an ash-free basis was 9.03 ± 0.05 kcal/g.

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Triglyceride fats extracted from subcutaneous or abdominal deposits had a combustible energy of 9.3 kcal/g ash-free weight. Johnston (1970) also measured the caloric value of fats extracted from adipose tissue (claviculo-coracoid fat pad) of small passerines; he obtained values of 8.2-9.2 kcal/g depending on the fat content of the adipose tissue (30-90% in Johnston's study, but reported to be as low as 7% by Odum, et al., 1964). I recommend that 9.0 kcal/g be adopted as the energy content of extracted lipids.

Combustible energy contents of lean dry fractions of various species of birds, based on bomb calorimetry, are presented in Table 3. None of the determinations based on ash-free lean dry weight are greater than

TABLE 3

Combustible Energy Contents of the Lean Dry Fraction of Birds.

Species ¹	Combustible energy (kcal/g)		Source
	Lean dry weight	Ash-free lean dry weight	
Japanese Quail chicks	4.30 ²		Brisbin and Tally, 1973
Red Jungle Fowl	4.80		Cummins and Wuycheck, 1971, quoting I.L. Brisbin, unpubl.
Guinea Fowl	4.84		"
Domestic Hen chicks	4.69		"
Double-crested Cormorant chicks	4.98 ⁵		Dunn, 1973
Dunlin chicks	5.1-5.3 ^{2,5}		Norton, 1973
Herring Gull chicks	4.36		Brisbin, 1965
Ringed Dove adults	5.00		Brisbin, 1969
nestlings	4.87 ± 0.04 ⁴		
Mourning Dove	5.14 ± 0.02 ⁴		Brisbin, 1968
Long-billed Marsh Wren adults		5.33 ± 0.06 ⁴	Kale, 1965
fledglings		5.15 ± 0.05 ⁴	
Tree Sparrow juveniles before molt	4.83	5.53	Myrcha and Pinowski, 1970
after molt	4.45	5.11	
Passerines (various species) ³	4.72	5.46	Odum, Marshall, and Marples, 1965

¹ Adult birds unless indicated otherwise.

² Values change with age.

³ Values obtained from fat birds (2.61 kcal/g live weight).

⁴ Standard errors of the mean (SE).

⁵ Extracted in petroleum ether only.

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5.5 kcal/g whereas we would expect values as great as 5.65 kcal/g, assuming the ash-free lean dry component is protein. Values of 5.3 and lower probably represent inefficient combustion or faulty ash determination. In this paper I will adopt the somewhat arbitrary figure of 5.5 kcal/g ash-free lean dry weight.

If we assume the average ash content of the body is 13% of the lean dry weight, we would expect combustible energy based on lean dry weight to be close to 4.9 kcal/g (5.65×0.87). Values for gulls and quail chicks (4.3-4.4) are seemingly too low, perhaps because of inefficient combustion, and values determined for Dunlin (*Calidris alpina*) chicks and doves are above 5.0, possibly because of inefficient fat extraction. The variation in direct calorimetric determinations of combustible energy and the frequent discrepancy between these and expected values suggests that indirect estimation of energy value from chemical components is quite reasonable.

Ash content of whole birds determined by combusting carcasses in a muffle furnace includes the mineralized portion of bones and salts dissolved in the body fluids. Expressed as a percent of lean dry weight, ash content varies between about 12 and 13.5% for a variety of species: Swainson Thrush (*Catharus ustulatus*) 12.26 ± 0.11 (SE), Wood Thrush (*Hylocichla guttatus*) 12.47 ± 0.10 (SE), Kentucky Warbler (*Oporornis formosus*) 12.02 ± 0.16 (SE) (Odum, Marshall, and Marples, 1965), Cactus Wren (*Campylorhynchus brunneicapillus*) 15.36 ± 0.30 (SE) (Ricklefs, 1974), Rufous-winged Sparrow (*Aimophila carpalis*) 12.77 ± 0.32 (SE), Common Tern (*Sterna hirundo*) 13.51 ± 0.03 (SE), Sooty Tern (*Sterna fuscata*) 13.48 ± 0.46 (SE), Coturnix Quail (*Coturnix coturnix*) (50-60 days) 13.23 ± 0.27 (SE), and Leach's Petrel (*Oceanodroma leucorhoa*) 12.73 ± 0.20 (SE) (unpublished). The rather high value for the Cactus Wren should be discounted because of the presence of a large ash component of unknown composition in the integument. The proportion of total body ash that occurs in bone material has been determined for several species; Rufous-winged Sparrow 65%, Common Tern 74%, Coturnix Quail 69%, and Leach's Petrel 75% (unpublished).

ADULT METABOLISM

Most aspects of adult metabolism have been thoroughly reviewed in other papers presented in this symposium. But I shall summarize basic patterns of adult metabolism here to provide a relative energetic scale for comparing reproductive processes and the metabolic performance of young.

Over a wide range of body size, most metabolic parameters are related to body weight by familiar power laws of the form

$$M = aW^b$$

or, in logarithmic form,

$$\log M = \log a + b \log W$$

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where M is some metabolic parameter, a is a constant, W is body weight, and b is an exponent, the "power" of the relationship, which describes how rapidly M changes with respect to W . If b lies between 0 and 1, M increases less rapidly than W . If b is greater than 1, M increases proportionately more rapidly than W . When b is 0, M is independent of body size. Negative values of b indicate that M decreases as W increases. Power relationships have the convenient property that when expressions with different powers of the same base (W) are multiplied, the exponents (b 's) are added. When one expression is divided by another, the exponent of the second is subtracted from the first. For example, if the metabolic rate of a whole bird is related to adult weight in proportion to $W^{0.7}$, metabolic rate per gram is proportional to $W^{-0.3}$ ($W^{0.7}/W^{1.0} = W^{0.7-1.0} = W^{-0.3}$).

STANDARD METABOLISM

Standard metabolism is determined under conditions that usually provide the lowest and most consistent measurement of metabolism, namely under post-absorptive conditions, within the thermoneutral zone (when it is called basal metabolism; Kendeigh, 1972), without activity (usually in the dark), and at a particular time during the diurnal cycle. Brody and Proctor (1932) initially estimated b as 0.640. Subsequent measurements on a wider range of species have changed the estimate to between 0.70 and 0.75 (King and Farner, 1961; Lasiewski and Dawson, 1967; Zar, 1968; Kendeigh, 1969). Since standard errors of b range from 0.04-0.11, we cannot make any precise statistical distinctions between reported values. Aschoff and Pohl (1970) presented the most carefully selected data set, and I will use their regressions of standard metabolism during inactive periods of the diurnal cycle on body weight in this paper. The pertinent equations are:

$$\text{Nonpasserines (17 studies) } b = 0.0193 \ W^{0.734}$$

$$\text{Passerines (14 studies) } b = 0.0317 \ W^{0.726}$$

where b is metabolic rate in kcal/hr per bird, W is body weight in grams. Standard errors of b are 0.067 and 0.044, respectively. For calculating metabolic rate on a daily basis, a should be 0.463 and 0.761, respectively.

METABOLIC COST OF TEMPERATURE REGULATION AND LOWER CRITICAL TEMPERATURE

Thermal conductance is a measure of the rate of heat loss from the body of a bird, usually expressed per unit weight or surface area. Conductance can be measured by the rate of decrease in body temperature of a dead bird for a known gradient between the temperature of the bird's body and the surrounding air. Conductance can also be estimated from the metabolic rate of the organism at air temperatures

TABLE 4
Relationships of Various Metabolic Properties (*M*) of Birds to Adult Body Weight (*W*) According to the Equation $M = aW^b$.

Metabolic property	Units	Weight basis	Sample	N	Weight range	<i>a</i>	<i>b</i>	Standard error of <i>b</i>	Reference
Standard									
metabolism	kcal/day	kg	all birds		0.125-17.6	74.3	0.744		King and Farner, 1961
"	"	"	nonpasserines	72	0.003-100	78.5	0.722	0.109	Lasiewski and Dawson, 1967
"	"	"	passerines	48		129	0.724	0.079	"
"	"	g	nonpasserines						
			active	17		91.0	0.729	0.066	Ashoff and Pohl, 1970
			resting	17		73.5	0.734	0.067	"
			passerines						
			active	14		140.9	0.704	0.058	"
			resting	14		114.8	0.726	0.044	"
"	kcal/hr	g	nonpasserines						
			resting	17		.0193	0.734	0.067	"
			passerines						
			resting	14		.0317	0.726	0.044	"
"	kcal/day	g	nonpasserines	17		.513	0.717	0.111	Kendeigh, 1969
			passerines	15		.882	0.693	0.062	"

TABLE 4 (continued)

Metabolic property	Units	Weight basis	Sample	N	Weight range	a	b	Standard error of b	Reference
Thermal conductance	$\frac{\text{ccO}_2}{\text{g}\cdot\text{hr}\cdot^\circ\text{C}}$								
(standard conditions based on metabolism)	$\frac{\text{kcal}}{\text{hr}\cdot^\circ\text{C}}$								
	$\frac{\text{kcal}}{\text{m}^2\cdot\text{hr}\cdot^\circ\text{C}}$								
(based on temperature decrease)	$\frac{\text{cal}}{\text{g}\cdot\text{hr}\cdot^\circ\text{C}}$								
	"								
	"								
Evaporative heat loss/standard metabolism	none								
Critical temperature gradient $\Delta T_e = T_b - T_c$	$^\circ\text{C}$								

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below thermoneutrality, if body temperature is constant and metabolic heat production exactly balances heat loss. By definition, conductance measures the heat lost across a body surface. Therefore, calculations of conductance should be based on surface temperature, and should be corrected for evaporative heat loss from the respiratory surfaces. In practice, surface temperature and evaporative heat loss are difficult and expensive to measure, and most conductance values are based on either body core cooling or total metabolism (see, however, Veghte and Herried, 1965, and Drent and Stonehouse, 1971).

Several authors have used metabolic rate data to calculate thermal conductance for a wide range of species. For example, Lasiewski, Weathers, and Bernstein (1967) calculated values of thermal conductance for live birds as

$$C = \frac{\text{metabolic rate}}{(\text{body-air temperature}) \times \text{body weight}}$$

C has the units (cal/g·hr·°C). The equation relating C to body weight (W) (Table 4) has the form of the power relationship presented above with b equal to -0.508 . Thermal conductance thus decreases approximately as the square root of body weight; the inverse of C , which is proportional to insulation, increases as the square root of body weight. Because the surface volume ratio of a sphere decreases as the $1/3$ power of body weight ($b = -0.33$) conductance should decrease at the same rate. Instead, it falls off more rapidly, suggesting that larger birds are relatively better insulated than smaller birds. To what extent this is caused by quantitative or qualitative differences in plumage, or by the insulating effects of the body itself on its core, is not known (see, however, Scholander, 1955).

Drent and Stonehouse (1971) calculated conductance from published metabolism data on a larger number of species, basing their values on body surface area. They also corrected metabolic rate for heat lost by evaporative water loss to obtain true values for the conductance of heat across the external body surfaces. They used an empirically determined, equation, often referred to as Meeh's formula,

$$S = 0.001 W^{2/3}$$

to determine body surface area (m^2) from weight (g). The slope of the logarithmic equation is -0.134 . One can convert Drent and Stonehouse's conductance values to a body weight basis by multiplying them by $.001 W^{-1/3}$ (the ratio of surface area (m^2) to weight (g)). The resulting conductance-body weight relationship has an exponent (b) of 0.464 , which is slightly lower than that obtained by Lasiewski, et al. (1967). The correction for evaporative heat loss should have produced a steeper slope because the proportion of heat loss due to evaporation decreases with increasing body size ($b = -0.160$; Drent and Stonehouse, 1971).

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Finally, Herreid and Kessel (1967) determined the rate of heat loss from dead birds that were either intact or defeathered by measuring the temperature drop of carcasses warmed to a given temperature and placed in cooler air. The value of b determined for feathered birds (-0.52) agrees well with that of Lasiewski, et al. (1967) although Herreid and Kessel's determinations of conductance are uniformly higher. Correcting for the specific heat of the body ($0.83 \text{ kcal/g} \cdot ^\circ\text{C}$; Hart, 1951), reduces this discrepancy.

The relationship between conductance and body weight in defeathered birds has a smaller exponent (-0.44) than that for intact birds, which suggests that the insulating value of plumage increases with body size. The thermal conductance of defeathered adult birds is of particular interest to understanding the ontogeny of thermoregulation in altricial nestlings, which lack feathers at hatching.

The lower critical temperature (T_c), below which birds under standard conditions must generate heat over and above basal metabolic levels to maintain their body temperatures, can be calculated from the equation

$$\Delta T_c = T_b - T_c = \frac{\text{standard metabolism}}{\text{weight} \cdot \text{conductance}}$$

where T_b is the body temperature. Heat lost by the evaporation of water is included in values for conductance. This equation is strictly valid only if the relationship between metabolism (M) and ambient temperature can be extrapolated through body temperature at $M = 0$. Assuming $b = 0.73$ for standard metabolism and -0.51 for conductance, the critical gradient (ΔT_c) should increase as the 0.24 power of body weight ($0.73 + .51 = 1.00$). The lower critical temperature is often difficult to determine from metabolism data, so we would not expect a precise conformance to our model. Based on Kendeigh's (1969) tabulation of lower critical temperatures, b is about 0.274 for nonpasserines and 0.454 for passerines. These values are greater than we would expect, but they conform to expectations (0.29 and 0.49) based on slopes of the relationships between metabolism and air temperature (approximately weight times conductance) presented by Kendeigh (0.439 and 0.236, respectively).

ROUTES OF ENERGY EXPENDITURE

Birds use energy in a variety of ways to perform the work of maintenance activity, temperature regulation, and production. The sum of these uses cannot exceed the individual's long-term intake of metabolizable energy if it is to survive; thus the allocation of energy to any one use affects the availability of energy for all other purposes. We may classify routes of energy expenditure, beginning with the ingestion of food, in the following way:

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Available	Use	Remainder
Ingested energy	Passage of non-digestible portion	Assimilated energy
Assimilated energy	Excretion of nitrogenous compounds in urine	Metabolizable energy
Metabolizable energy	Digestion and processing of foods into metabolically useful forms (specific dynamic action)	Available energy
Available energy	Basal metabolism, temperature regulation, activity	Productive energy
Productive energy	Work of biosynthesis	Production

The difference between ingested energy and available energy is primarily a property of food quality. It is affected by the design of the organism only to the extent that evolved mechanisms, often involving a gut flora and fauna, aid the digestion of particular substances. The digestibility of foods is a very complex subject based primarily on empirical observation. A general survey of assimilation efficiencies ($100 \times \text{assimilated energy} / \text{ingested energy}$) indicated values of 70-80% for insect diets, up to 90% for meat and fish diets, up to 80% for seeds, 50-90% for aquatic vegetation, up to 60-70% for young (growing) terrestrial vegetation, 30-40% for mature foliage, and about 15% for wood (Ricklefs, 1973b). The availability of energy to birds feeding on various foods falls within these ranges (Table 5).

TABLE 5

Availability of Energy to Birds Feeding on Various Foods (adapted from Dunn, 1973).

Food	Availability of energy (%) ¹	Reference
Pine needles	30	Pendergast and Boag, 1971
Willow buds and twigs	32	Moss, 1973
<i>Vaccinium</i> fruits	31	Pullianinen, et al., 1968
Wheat grain	76	Murton, et al., 1963
Seeds	80	Gibb, 1957
Insects	66	Gibb, 1957
Grasshoppers	69	Schwartz and Zimmerman, 1971
Whiting (fish)	79	Kahl, 1964
Horse mackeral	81	Uramoto, 1961
Various fish	82	Dunn, 1973

¹(Metabolizable energy/ingested energy) x 100.

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The loss of energy due to excretion of nitrogen has already been discussed. It should be pointed out that nitrogen eventually destined for production should not be included in estimates of excretory nitrogen loss.

SPECIFIC DYNAMIC ACTION

Assimilated food stimulates the production of heat independently of other changes in the behavior of the organism. This increment of metabolism, which is characteristic of the amount, and type, of food ingested, is called the calorigenic effect of food, or specific dynamic action (SDA), and it is associated with the metabolic work of digestion and molecular transformation of foodstuffs into forms suitable for the organism's use (Wilhelmj, 1935; Brody, 1945; Kleiber, 1961).

The amount of specific dynamic action is directly related to the amount of food ingested. But most authors measure the calorigenic effect of food by the elevation of metabolism above standard post-absorptive levels in organisms fed maintenance diets. As one would expect, SDA varies considerably with the subjects and conditions of the experiment. The following ratios of SDA/BMR are typical: 50 to 60% in adult male North Holland Bluefowls at 10°C (Romijn and Lokhorst, 1966); 28 to 43% depending on temperature (38-21°C) in White Leghorn chicks, 6-15 days old (Kleiber and Dougherty, 1934); 28.5% in 25-day old Tippler pigeons at 30°C (Riddle, Nussman, and Benedict, 1932); 15 to 18% in adult male chickens fed gelatin and casein, respectively (Barott, et al., 1938).

Specific dynamic action is independent of the species and size of animal; it is related, instead, to the kind and amount of food eaten (Kleiber, 1961). About 80% of the SDA originates in the viscera, suggesting that SDA represents the work of catabolizing foodstuffs, particularly protein, rather than increased activity stimulated by feeding (Brody, 1945). The fact that amino acids injected directly into the bloodstream have a calorigenic effect similar to that of ingested proteins indicates that the work of digestion is not a major part of SDA (Brody, 1945). Careful measurements of metabolism under experimental dietary regimes have shown that the SDA of various food stuffs ranges from about 6-31% of the gross energy of the food itself, and would elevate the standard metabolism of animals between 6 and 45% if the maintenance needs of the organism were satisfied exclusively by that foodstuff (Brody, 1945; Kriss, et al., 1934). These relationships are shown in the following table.

Food	SDA (% of food)	Elevation of standard metabolism (%)
Protein	31	45
Starch	23	29
Olive oil	17	20
Fat	13	15
Sucrose	6	6

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Kleiber (1961) suggested that only catabolized protein has a calorogenic effect; protein accumulated in tissue has a negligible specific dynamic action. But Kriss, et al. (1934) were able to show indirectly, in an elegant series of feeding experiments on white rats, that body protein and fat used for metabolic purposes during periods of fasting have a calorogenic effect similar to that of ingested food. Therefore, basal metabolism includes the SDA of metabolized body tissues and fat reserves. This partly explains the somewhat confusing results of Barott, et al., who found that chickens fed pure protein exhibited an apparent SDA of only 15 to 18%. It is also apparent that values for SDA which are much greater than 10 to 20% for diets with a relatively low proportion of protein indicate that metabolism is stimulated over and above the SDA or that the food is processed more readily than its energy is released in metabolism.

The duration of the calorogenic effect of food, and thus the period after feeding before standard conditions are reached, apparently varies with age, being longer in older chicks (Barott, et al., 1938), and with the type of food. Romijn and Lokhorst (1964) determined that the domestic fowl requires two full days to reach standard conditions. In Barott, et al.'s (1938) experiments, in which fasting male chickens were given a single feeding of either gelatin or casein, the initial elevation of metabolism was only 15 to 18% but the calorogenic effect of that feeding persisted for 1 to 2 days. Although most authors assume that small songbirds reach a "post absorptive" state within 2 to 4 hours after their last feeding, I have seen no direct experimental verification.

TEMPERATURE REGULATION AND ACTIVITY

The metabolic requirements of temperature regulation and specific activities are almost unknown for free-living adult birds. One can do little more than relate metabolism to these factors under laboratory conditions. We have already reviewed the metabolic response of adult birds to ambient temperature. The equations for thermal conductance in Table 4 indicate that low temperatures place less stress upon large birds than small birds. (The opposite is true for the problem of heat dissipation at high ambient temperatures or at high levels of activity). The metabolic requirements of temperature regulation are also influenced by plumage quality (Scholander, et al., 1950; Scholander, 1955) and body posture (Hart and Heroux 1955, Kontogiannis 1968). The energy requirements of activity and locomotion have been reviewed by Calder, King, and Tucker in this symposium. These requirements will be considered with respect to the energetics of nestling development and the foraging activities of parent birds later in this paper.

PRODUCTION EFFICIENCY

The biosynthesis of materials, whether structural components of tissues or stored reserves, has a metabolic cost that is an important

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component of the energy budgets of egg-laying females and growing young. The cost of production is virtually impossible to measure directly because synthetic processes cannot be separated from other functions of the organism. The problem of measuring production efficiencies has been approached in a variety of ways, each providing a slightly different type of information. We shall define production efficiency, often referred to as partial, or net, production efficiency as

$$\text{Production efficiency} = \frac{\text{energy content of production}}{\text{energy content of production} + \text{cost of biosynthesis}} \times 100.$$

The overall efficiency of embryonic growth can be estimated as the energy in the full term embryo divided by the initial energy content of the egg (minus energy incorporated into shell membranes). This index does not differentiate the maintenance metabolism of the embryo from the work of production, but it does provide a minimum estimate of production efficiency. Brody (1945) reported an index of 62% for the chicken, and from 51 to 65% for other types of animals. The overall efficiency of embryonic growth of the Green Iguana (*Iguana iguana*), whose embryonic period is about 100 days (compared to 21 for the chicken), is 48% (Ricklefs and Cullen, 1973).

Energetic efficiencies have been calculated for the production of milk and eggs by comparing the difference between energy intake of producing and nonproducing animals with the caloric value of their production; corrections are made for changes in body weight if necessary. Brody (1945) quotes values of 61% for the efficiency of milk production in cattle and 77% for egg production in laying hens. El-Wailley's (1966) value of 75% for egg production in the Zebra Finch (*Taeniopygia castanotis*) is remarkably similar to that for hens.

Efficiencies of production of body tissue may be calculated by comparing food intake and tissue accumulation in a series of animals that grow by different amounts. This technique requires a complete carcass analysis at the end of the experiment and a reasonable estimate of carcass composition at the beginning of the experiment. The slope of the relationship between energy accumulated during growth and metabolizable energy intake during the growth period is the production efficiency. Calculated in this manner, values for production efficiency vary widely: for example, 62-65% for fat deposition in the Bobolink (*Dolichonyx oryzivorus*) (Gifford and Odum, 1965), 45-63% for growth in cows, and 52-88% for growth in pigs (Brody, 1945).

Partial efficiency of production appears to vary with age, temperature, composition of diet, and type of substance accumulated. Oslage and Fliegel (1964) determined that the partial efficiency of production in growing swine decreased from 80-85% (2-8 kg body weight) to 63% (170 kg body weight). Over this size range, the retention of ingested nitrogen in tissue accumulation decreased from 60 to 24% and fat

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deposition increased in relative importance. Kleiber and Dougherty (1934) found that the partial efficiency of growth in young chickens (6-15 days) was greatest (72%) at 38°C, and decreased to 57% at 21°C and to about 60% at 40°C.

Efficiency of production depends partly on how much molecular rearrangement must occur. It is less efficient to make fats from proteins than from other fats or from carbohydrates. For example, the efficiency of production of fattening cattle is 63-64% when fed carbohydrate or fat, but only 48% when fed protein (Kleiber, 1961). The fact that production efficiencies for fattening pigs are generally higher for all types of foodstuffs (72-93%), but relatively low for sugar (72%), indicates that substantial differences in production efficiency may occur between species.

Kielanowski (1964) factored out separate efficiencies for protein accumulation and fat deposition in growing lambs and pigs by a multiple regression analysis of metabolizable energy intake, number of days on test, and protein and fat deposited. The efficiency of protein production was found to be 80% for lambs and 75% for pigs, although the theoretical efficiency of protein production, based on biochemical consideration, is more than 90% (Schiemann, 1963; Blaxter, 1962). Efficiency of fat production in Kielanowski's experiments was 63 and 82% for lambs and pigs, respectively.

The range of values reported for production efficiencies in the literature, and the clear indication that efficiency varies with species, diet, age, temperature, and other factors, make it difficult to adopt anything but an arbitrary, representative value for the calculations in this paper. I will use 75% for the efficiency of all aspects of avian production related to reproductive activities. Thus, for energy accumulated in tissues, eggs, or stored reserves, an additional one-third is assumed to have been expended in the work of production.

PRINCIPLE OF COMPENSATION

Rubner (1910) suggested that heat generated by specific dynamic action, the work of production, and activity could be used for temperature regulation. Therefore, any metabolic activity above standard metabolism would elevate overall metabolism within the thermoneutral zone and would thus decrease the lower critical temperature. Below the lower critical temperature, heat generated by activities over and above basal processes would compensate the loss of heat to a cold environment and would correspondingly reduce the production of energy specifically for temperature regulation. According to this principle, activity should not increase the metabolic rate of animals at air temperatures below their lower critical temperature.

Available evidence does not support Rubner's principle, however. For example, Kleiber and Dougherty (1934) found that the calorogenic effect of food, measured as the percentage increase of metabolism in fed chicks (6-15 days of age) over fasting levels, actually increased from

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28 to 43% over the temperature range of 38° to 21°C. Rubner's principle would have predicted that the apparent calorogenic effect of food would have decreased with lower temperature as an increasing proportion of the SDA was used to compensate heat loss. Kleiber and Dougherty suggested that the discrepancy between their observations and Rubner's principle could have been caused partly by the huddling behavior of chicks at low temperature, which reduces heat loss. But the metabolism of the chicks doubled between 38° and 21°C and the cost of thermoregulation should have completely absorbed the SDA. Kleiber and Dougherty's results indicate that heat production for the regulation of body temperature is largely independent of other metabolic activity. The increase in apparent SDA at lower temperatures would occur if a greater proportion of assimilated energy was metabolized to produce heat at lower temperatures rather than to support growth. If SDA is calculated on the basis of heat output rather than assimilated energy, values are more similar (42% at 38°C and 53% at 21°C) than when they are based on assimilated energy (28 and 43%, respectively).

The independence of heat production for temperature regulation from other metabolic activities is further supported by the observations of Hart and Heroux (1955) on lemmings and rabbits, of Kontogiannis (1968) on White-throated Sparrows (*Zonotricha albicollis*), and of Pohl and West (1973) on Common Redpolls (*Acanthis flammea*). Imposed locomotory activity in these species increases metabolism by a constant amount that is independent of temperature below the thermoneutral zone. The apparent inapplicability of Rubner's compensation principle has important consequences for the budgeting of energy at low temperatures. The energetic cost of activity apparently is not absorbed by the need for temperature regulation and, furthermore, activity increases the conductance of the organism by precluding heat conserving postures.

CONCEPT OF PRODUCTIVE ENERGY

Kendeigh (1949) proposed that the amount of energy which animals could mobilize to supply their energetic needs had a fixed upper limit determined by the metabolic machinery of the organism. The difference between the maximum potentially available energy and the energy required to keep the adult alive (basal metabolism, SDA, foraging activity, temperature regulation, etc.) represents the portion available for productive processes, such as growth, egg formation, and incubation. If the bird does not have sufficient "productive energy" to sustain these activities, reproduction cannot occur. Kendeigh's principle has been important to the development of ideas about reproductive energetics because the principle states a clear relationship between reproduction and ambient temperature (hence the cost of temperature regulation to the adult).

The productive energy concept is outlined in its simplest form in Figure 1, after West (1960). Available energy (see page 167), West's

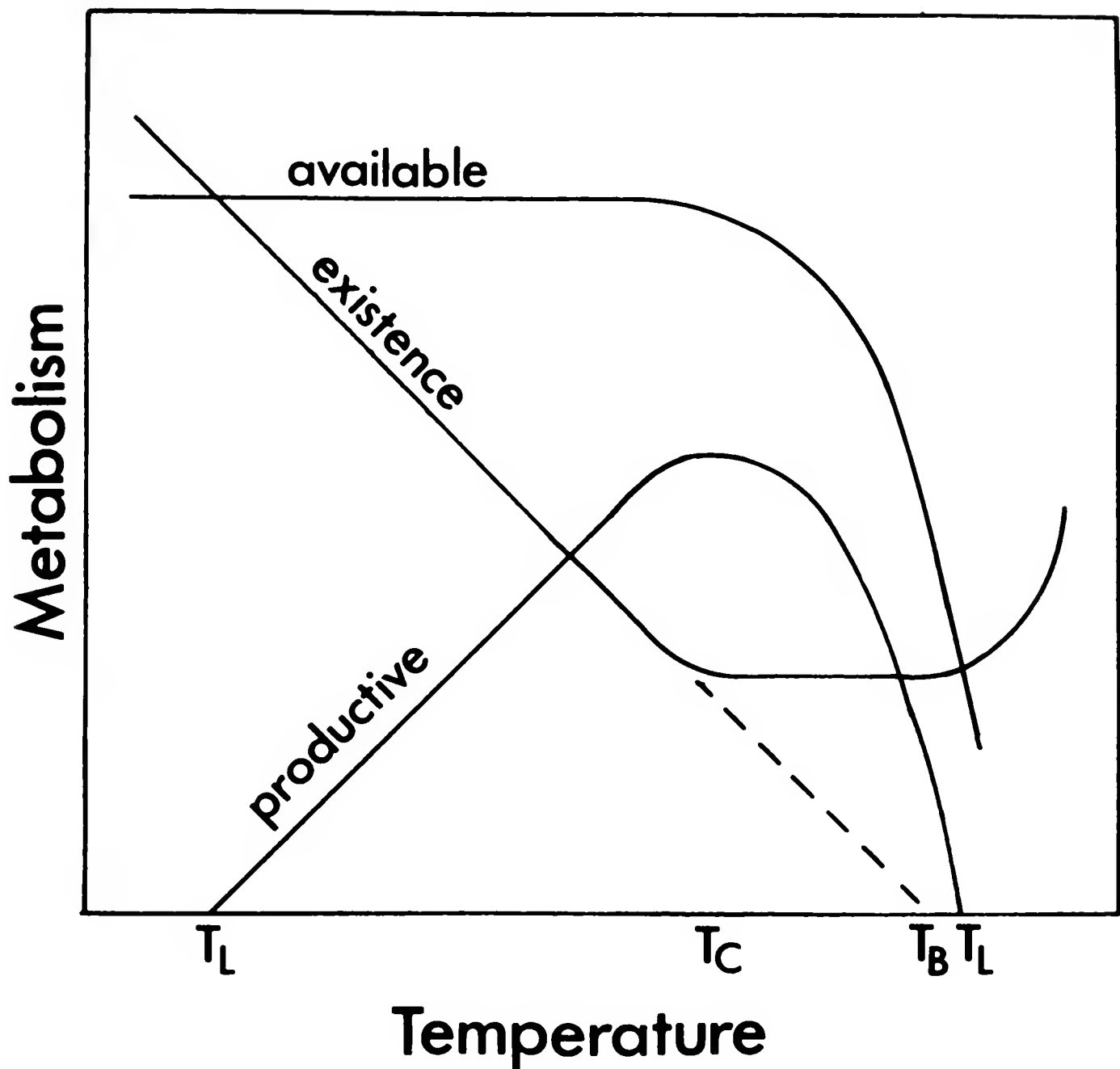


FIG. 1. Simplified model of the relationship between productive energy (available energy minus existence energy) and ambient temperature (see text). T_B = body temperature, T_C = lower critical temperature, T_L = upper and lower temperature limits of long-term existence.

“potential energy,” is assumed to be constant over a wide range of temperature, but decreases rapidly as ambient temperature approaches body temperature and heat dissipation becomes more difficult (see Kendeigh, 1972). The difference between available energy and that used for basal metabolism, activity, and temperature regulation (“existence energy”), is the productive energy.

Several authors (e.g., Kendeigh, 1963; Drent, 1970) have sought to compare the energy requirements of various processes to productive energy to determine environmental limits to productive activities. The concept of productive energy is therefore basic to our understanding of reproductive behavior. But the concept has been so simplistically applied to natural situations that it has likely caused more confusion than it has provided clarification.

The amount of energy available to adults may be limited by (a) the work capacity of various tissues, (b) the ability to mobilize energy

from stored reserves, (c) rates of digestion and assimilation of food-stuffs, or (d) foraging behavior and food availability. Each of these limits has different implications for the productive energy concept.

Kendeigh and his students and colleagues maintain that available energy is limited by the rate at which energy can be metabolized by the bird, which is largely independent of environmental conditions or of the purpose for which the energy is released. Thus an increase in activity or cost of temperature regulation directly reduces the energy available for other purposes. It is further assumed that potentially available rates of energy mobilization can be determined by cold stress. The metabolic rate measured over a period of several days under cold stress, usually at the lowest temperature tolerated by the bird, represents the maximum metabolic capacity of the organism.

Kendeigh's model is supported by several lines of evidence. First, when birds are exposed to temperatures below the long-term critical minimum they apparently die of starvation rather than from a breakdown of homeothermic capacity (Kontogiannis, 1968). This suggests that life is limited by the energy assimilating system rather than the heat generating system. Second, forced activity increases the lower lethal temperature but the maximum available energy measured does not change (Kontogiannis 1968; Hart and Heroux, 1955). Thus, White-throated Sparrows maintained without exercise attained a maximum metabolic rate of 34 kcal/day at -29°C ; birds forced to exercise reached the same level of metabolism at -11°C , and could not tolerate lower temperatures.

These data are open to alternative interpretations that greatly change the meaning of the productive energy concept. If available energy, measured under conditions of cold stress, is actually limited by the heat generating capacity of the muscles, ambient temperatures below the limit of tolerance would cause hypothermia (see Hart and Heroux, 1955), which in turn could lead to dysfunction of energy acquisition and mobilizing processes. A bird may starve to death, but the primary cause could be hypothermia rather than some inherent limit to energy assimilation. Activity can substantially reduce homeothermic capacity at low temperature by reducing insulation (Hart and Heroux, 1955).

If metabolic and productive processes are limited independently at the tissue level, each process much be considered separately; egg production rates would be limited by the metabolic capabilities of ovarian and oviductal tissues, for example. Heat production by muscle tremors (West, 1965) and the power output of locomotion could have different ultimate limits even though both functions reside in the same tissue. For example, whereas the maximum metabolic rate of White-throated Sparrows under cold stress (34 kcal/day) is only 4 to 5 times basal metabolism (Kontogiannis, 1968), metabolic rates of various species of birds in sustained flight are 6 to 16 times standard metabolism (Dolnik, 1967; LeFebvre, 1964; Tucker, 1970 and this volume;

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Utter and LeFebvre, 1970). One could argue that flying birds operate under a temporary energy deficit, but many species fly for long periods of the day, more or less continuously, without starving.

Food availability and procurement also could limit metabolic rate. Rate of food procurement depends on three factors: food availability, which is a property of the environment; percentage of time spent foraging, which is partly related to reproductive strategy, and foraging effort, which must remain within the constraints of energy mobilization and heat dissipation.

Further discussion of productive energy will be deferred until specific components of reproductive strategy are considered. But at the outset, it is clear that we must exercise caution in formulating a concept of productive energy for the limitation of reproductive behavior.

ENERGETICS AND THE REPRODUCTIVE CYCLE

The stages of the reproductive cycle provide a convenient scheme of organization for reviewing what we know of the energetics of reproduction. But we are also interested in broader questions about the role of energetics in the evolution of the reproductive strategy. These questions often transcend individual stages of the reproductive cycle, and often relegate energy to a less influential role than time budgeting and strategies of survival.

Before the first egg is laid, birds engage in activities, including territorial establishment and defense, courtship, and nest building that are crucial to reproduction but are not directly involved in the parent-offspring relationship. Such preparatory activities are generally ignored in studies of reproductive energetics, partly because they are thought to exert little direct influence on the success of parents in raising their young, and partly because the energetics of these activities cannot be measured easily. Nevertheless, some preparatory activities do affect development and parental care. Territoriality influences the time budgets of the adults and establishes food availability during the reproductive cycle in many species. Nest building influences the energetics of incubation, brooding, and nestling thermoregulation. Gonadal recrudescence occurs during the preparatory period, but nonetheless has received attention in reviews of reproductive energetics (e.g. King, 1973) and is relatively easy to measure.

The nesting cycle may be divided into several distinct periods with different types of energy demand. During the egg formation period (which includes the egg-laying stage of the nest cycle), provisioning the egg with fat and protein secreted through the follicle cells is the primary energy demand. Furthermore, the added weight of reproductive organs and developing eggs may increase the female's energetic cost of locomotion. Incubation requires the production of body heat and its efficient transfer to the egg. Internal mobilization of energy is the dominant feature of incubation energetics, but factors external

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to the adult—the clutch of eggs and its microenvironment—become relatively more important. During the nestling period parents deliver energy directly to their young with little preprocessing of food in most species. During the nestling period our consideration of internal aspects of energetics is centered upon the young, although parental care influences patterns of energy use by young, and adults also perform work to gather food. The role of energetics in reproductive strategy wanes as the young assume independence, although its influence may continue long afterward if parents accept energy deficits during the reproductive cycle or if they postpone other activities, such as molt and migration.

The young change rapidly during their period of dependence, but it is difficult to assign them to rigid stages of development. We may refer to young as nestlings until they leave the nest or, in the case of semiprecocial species that are fed by their parents, until they can fly. Young may be called fledglings until they are independent of parental care, juveniles until the postjuvenile molt, and immatures until their first reproductive season. These labels are applied only for convenience, however, and do not represent uniformly well-defined categories (see Van Tyne and Berger, 1959).

During the reproductive cycle patterns of energy use shift their emphasis from internal mobilization to external energy delivery. But at all stages organisms must perform work to reproduce (egg formation, heat production, food delivery, and the like) and they must also procure and metabolize energy to perform that work. Thus, the rate at which food is delivered to the young is limited just as much by the ability of the adult to perform the work of foraging as it is by the ecological availability of food. Budgeting time for foraging may be as important a determinant of incubation behavior as heat production, heat transfer, and the insulative properties of the nest. The parent-offspring complex is a bounded system with only one important source of energy—the foraging behavior of the adult—to support a variety of energetic functions.

The considerations outlined above set the stage for tackling the major energetic problems of reproduction. What factors determine the level of productive energy available during the nesting cycle? How do strategies of energy management of the adults and young maximize the efficiency of reproduction? To what extent do energy storage and deficit energy utilization affect patterns of energy budgeting? To what extent do energetic considerations determine growth rates of the young and their acquisition of independence? We shall return to these questions in the discussion at the end of this paper. The sections that follow outline patterns of energy utilization during the various stages of the nesting cycle, including egg formation, incubation and brooding, nestling development, adult requirements for foraging, energy storage and utilization, and the energy requirements of molt.

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ENERGETICS OF EGG FORMATION

Gonadal growth and egg formation are the first energy-requiring processes to occur during the nesting cycle that are directly related to the production of the young. Surprisingly little is known about this phase of reproduction. Prior to King's (1973) review, energetic aspects of egg formation had received little attention. Most of our information comes from analysis of developing gonads and eggs in adults collected up to the point of egg laying. These studies have centered primarily on the morphology of the gonads and ova, although a few workers have tested and experimentally induced effects of egg formation on adult females. In this section I will review what is known of the energetics of gonadal growth and egg formation, the caloric value of eggs, and the follicular growth rate; I will then relate these energetic considerations to patterns of egg laying and clutch size.

GONADAL GROWTH: MALES

King (1973) calculated the energetic cost of testicular growth from available data on testis size and growth rate. Weight increases of testes between resting and maximum size averaged $0.93\% \pm 0.60$ (SD) of adult body weight, with a range of 0.31% (Chukar, *Alectoris chukar*) to 2.25% (White-crowned Sparrow). King assumed the energy content of testes to be 2 kcal/g wet weight (which is probably too high) and the efficiency of synthesis to be 70% ; from these estimates he calculated that the maximum rate of testicular growth required an energy expenditure of 0.2% of basal metabolism (BMR) for the California Quail and 0.3% BMR for the Ring-necked Pheasant (*Phasianus colchicus*). Testis recrudescence is, therefore, a relatively minor energetic event.

The calculations presented in Table 6 substantially confirm King's conclusions. Mature testes comprise $1.8\% \pm 1.4$ (SD) of adult weight in eight species, with a range from 0.44% for the California Gull (*Larus californicus*) to 4.3% for the Starling (*Sturnus vulgaris*). Testicular growth rates were determined from collections of males over fixed time intervals. Only intervals of most rapid growth are presented in Table 6. Reproduction is so highly synchronized in populations of these species that periodic sampling probably can be used to estimate the growth rate of an individual's testes accurately. Assuming the caloric value of testes to be 1.9 kcal/g (based on an estimated tissue composition of 70% water, 25% protein, and 5% fat) and a production efficiency of 75% , the average caloric equivalent of the rapid phase of gonad growth is 0.95% BMR ± 0.61 (SD) (Table 6).

Another energetic consideration for males is the production of sperm. Few measurements of sperm production are available. Arscott and Parker (1963) reported daily semen production of about 0.6 ml in 2.6 kg male chickens which, at an energy content of even 2 kcal/cc, would represent only 0.8% BMR.

TABLE 6
Estimates of the Energy Requirement of Testicular Growth.

Species	Adult weight(g)	Gonad weight(g) ¹	% Adult weight	Days of growth ²	Growth rate		% BMR ⁴	Reference
					g/day	kcal/day ³		
California Gull	1000	4.48	0.44		—			Johnston, 1956
Ring-necked Pheasant	1316	8.22	0.62	27	0.153	0.39	0.43	Greeley and Meyer, 1953
Bank Swallow	13.7	0.22	1.57		—			Petersen, 1955
Starling	82.0	3.88 ⁵	4.73	11	0.147	0.37	1.98	Bissonette and Chapnick, 1930
Red-winged Blackbird	60.5	1.91	3.16	15	0.036	0.091	0.61	Wright and Wright, 1944
House Sparrow	27.2	0.40	1.47		—			Kendeigh, 1941
House Finch	19.8	0.17	0.86		—			Hamner, 1968
White-crowned Sparrow	27.0	0.44	1.63	10	0.025	0.063	0.76	King, et al., 1966

¹ Combined weights for both testes. No correction has been made for changes due to preservation. Kern (1970) determined that fresh weight = 0.36 + 1.38 fixed weight for the White-crowned Sparrow.

² Shortest period over which rapid growth was estimated, not the total period for gonadal growth.

³ Assuming 1.9 kcal/g wet weight and 75% production efficiency.

⁴ BMR calculated by equations in Aschoff and Pohl (1970); see Table 4.

⁵ Values are volumes in cc; I assume here that 1 cc = 1 gram wet weight.

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GONADAL GROWTH: FEMALES

King (1973) found that for a variety of species the combined weights of the ovary and oviduct increased by $6.07\% \pm 0.53$ (SD) adult body weight (range 5.54 to 6.66%) between resting and maximal size (i.e., a functioning, but nonovulating ovary). King estimated that the maximum combined growth rate of both organs in the California Quail (*Lophortyx californicus*) is 0.52 g/day, or 1.48 kcal/day (7.1% BMR), assuming 2 kcal/g and 70% production efficiency.

My calculations (Table 7) similarly indicate that gonad and oviduct growth carries a relatively greater energy demand for females than for males. Compared to egg formation (see below) the expenditure of an average of 2-13% BMR, even over a prolonged period, cannot be a major drain on the individual's metabolic capacities.

EGG COMPOSITION

Ornithologists have long known that egg composition varies among species and bears a consistent relation to the type of development exhibited by the young (Romanoff and Romanoff, 1949; Nice, 1962). Precocial species have larger yolks (30-40% of egg weight) and heavier shells (10-15%) than altricial species (yolk 15-25% and shell 5-10%) (Asmundson, et al., 1943, Romanoff and Romanoff 1949). In waterfowl (Anatidae) the yolk comprises about 40% of the egg contents, with a range between 37 and 49%, but the proportion of yolk is not related to the absolute size of the egg or to the size of the egg relative to adult weight (Lack, 1968; Siegfried, 1969). The megapodes (Megapodiidae) represent an extreme example of the precocial condition (yolk 62%; Nice, 1962); semiprecocial gulls and terns appear to be intermediate between altricial and precocial species (yolk 26-30%; Collins and LeCroy, 1972). With increasing egg weight the weight of the shell tends to increase as a proportion of the total weight while the proportion of yolk decreases. These relationships are more marked in altricial species than in precocial species (Table 8). The relatively greater proportion of yolk in the eggs of precocial species is related to the fact that precocial young hatch with an energy reserve derived directly from the egg yolk. The embryos of precocial species also may require relatively more maintenance energy during their prolonged incubation periods than the embryos of altricial species. These topics will be considered in more detail later.

To complete the picture of the energy content of eggs, we must consider dry weights and the relative amounts of protein and lipid in the dry substance of the egg. The albumen (white) of the egg consists mostly of water (86-90%) and protein. The egg whites of altricial species contain slightly less dry matter (10.5%) than the egg whites of precocial species (13.2%; Romanoff and Romanoff, 1949). Yolk contains relatively less water (50% in precocial land birds, 44% in

TABLE 7
Estimates of the Energy Requirements of Ovary and Oviduct Growth.

Species	Adult weight(g)	Mature organ weight(g) ¹	% Adult weight	Days of growth ²	Growth rate $\frac{\text{g/day}}{\text{kcal/day}}^3$	% BMR ⁴	Source
Mallard	1047	21.9	2.1		—		Johnson, 1961
		39.1	3.7		—		
California Quail	140	3-9	4.3	30	0.117	1.7	Lewin, 1963
		3-7	3.6	30	0.167	1.9	
Gambel Quail	167	3-4	2.1	30	0.117	1.5	Raitt and Ohmart, 1966
		3-5	2.4	30	0.133	1.4	
White Leghorn Chicken	1800	51.8	2.9		—		Romanoff and Romanoff, 1949
		78.1	4.3		—		
Pheasant (ovary only)	1050	31.0	3.0	7	1.85	6.1	Nagra and Buss, 1959
Pheasant (ovary only)	1000	33.0	3.3	21	1.52	5.2	Kirkpatrick, 1944
Bank Swallow	13.7	0.514	3.8	7	0.071	3.5	Petersen, 1955
		1.500	10.9		0.233	9.2	
White-crowned Sparrow	27	0.326	1.2	15	0.020	0.6	King, et al., 1966
		0.9-1.0	3.5	(15)	0.060	1.4	
Starling	76	0.43	0.6		—		Ricklefs, unpubl.
		4.63	6.1		—		

¹Ovary listed first, oviduct second.

²Shortest period over which rapid growth was estimated, not the total period for gonadal growth.

³Based on caloric equivalents of Starling ovaries and oviducts (1.87 and 1.52 kcal/g wet weight (unpublished)) and a production efficiency of 75%.

⁴BMR calculated by equations in Aschoff and Pohl (1970), see Table 4.

TABLE 8
Relationships of Proportional Parts of Birds' Eggs to Egg Weight (after data in Asmundsen, et al., 1943 and Romanoff and Romanoff, 1949).

Mode of development	Number of species	Range in egg weight (g)	Geometric mean weight(g) ¹	Proportional weight of		
				White	Yolk	Shell
Precocial	15	10-1400	64.8	0.540	0.343	0.114
Altricial	14	0.5-140	5.89	0.725	0.197	0.070

Regression equations for proportional weight on egg weight. ²											
			White			Yolk			Shell		
			r	a	b	r	a	b	r	a	b
Precocial	-0.123	.553	-.0054 ± .0059	-0.186	.361	-.0119 ± .0087	0.713	.0851	0.0691 ± .0209		
Altricial	0.633	.697	.0219 ± .0264	0.802	.249	.1320 ± .0649	0.761	.057	0.1162 ± .083		

¹Calculated from the average of the logarithms of egg weight.

²Constants are those of the logarithmic equation $x = aW^b$; r is the correlation coefficient of the regression; the standard error of b is also given; based on 15 precocial species and 14 altricial species.

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waterfowl, and 57% in altricial species) and its dry matter is distributed between fat and protein roughly in the proportion of 2:1.

The composition of eggs of several species is summarized in Table 9. For the energetics of egg formation the most important factors are the caloric value in kcal/g fresh egg weight and the protein/calorie ratio. Additional direct estimates of the caloric values of whole eggs are available: Herring Gull, 1.68 kcal/g wet weight of contents (Drent, 1970); Long-billed Marsh Wren (*Telmatodytes palustris*), 1.11 kcal/g (Kale, 1965); Tree Sparrow (*Passer montanus*), 1.02 kcal/g (Mackowicz, et al., 1970); and House Sparrow (*Passer domesticus*), 1.10 kcal/g (Tangl, 1903). Kendeigh, et al.'s (1956) value of 1.05 kcal/g for the House Wren (*Troglodytes aedon*) is based upon erroneous estimates, even though it is a reasonable value. A few miscellaneous values round out this survey: Norton (1973) reported values of 7.3 and 7.6 kcals/g dry weight for the contents of eggs of *Calidris alpina* and *C. bairdii*. Assuming protein contains 5.65 kcal/g of combustible energy and fat contains 9.5 kcal/g, percentages of fat in the dry weight of the egg can be calculated by the formula

$$\% \text{ fat} = \frac{\text{kcal/g} - 5.65}{9.5 - 5.65} \times 100$$

Percentages of fat calculated from Norton's data (43 and 51%, respectively) are rather similar to those of other precocial species (46-50%; Table 9). Drent's (1970) value of 6.91 kcal/g dry weight for Herring Gull egg contents suggests a composition of 33% lipid and 67% protein, which is similar to that of altricial species. Comparable values for the Mourning Dove (*Zenaidura macroura*), Starling, and Brown Pelican (*Pelecanus occidentalis*) are 37, 35 and 30%, respectively. Reid (1971) calculated the proportions of water in the yolk and white of one Kiwi (*Apteryx australis*) egg to be 43.3 and 87.9%, respectively, which is close to the composition of waterfowl eggs.

In summary, caloric values of eggs in kcals/g fresh weight range from 1.0-1.1 for small altricial species to about 1.65 for precocial land birds and 1.75 or more for waterfowl. Caloric values of yolk range from 3.5 for altricial land birds to 4.0-4.2 for precocial land birds and about 4.4 for waterfowl.

FOLLICULAR GROWTH RATE

The energy requirement of egg formation depends on the rate at which the egg is formed as well as on the energy content of the egg. In birds egg formation may be divided into two phases. Yolk formation occurs in the developing follicle in the ovary and white formation occurs in the oviduct (see Romanoff and Romanoff, 1949). Among species that lay one egg each day, the white is deposited around the yolk in a period of less than 24 hours and thus the daily rate of egg white formation is equivalent to the albumen content of a single egg.

TABLE 9
Composition and Energetic Equivalents of Eggs.

Species	Mourning				Brown				Guinea			
	Starling	Dove	Pigeon	Pelican	Chicken	Chicken	Turkey	Fowl	Duck	Goose		
Source	1	1	2	3	4	5	5	5	5	5		
Number of eggs	12	4	6								200	5
Fresh weight (g)	7.20	6.413	17.0	92.1	58.0	57.7	85	40	80			
Shell weight (g)	0.46	.432	1.38	11.2	6.4	6.1	10.0	5.04	9.6			
% egg	6.4	6.74	8.1	12.2	11.0	10.6	11.8	12.6	12.0			
Yolk weight (g)	1.22	1.883	3.9	24.1	17.4	18.7	27.4	13.0	26.3			
% egg	16.9	29.36	22.9	26.2	30.0	32.4	32.2	32.5	32.8			
water (%)	57	61.4	55.7	66	49	48.6	48.3	49.2	44.8			
lipid (%)	27	21.8	29.7	23	34	32.6	33.2	33.0	35.2			
protein (%)	16	16.8	12.4	11	17	16.6	16.3	16.0	17.7			
carbohydrate (%)	—	—	1.2	—	—	1.0	0.9	0.8	1.1			
inorganic (%)	—	—	1.0	—	—	1.1	1.3	1.0	1.2			
kcal ⁶	4.24	5.687	13.74	64.64	72.91	75.45	111.65	52.51	113.81			
kcal/g	3.48	3.02	3.52	2.69	4.19	4.03	4.07	4.04	4.34			
White weight (g)	5.08	3.567		60.8	34.2	32.9	44.2	19.9	40.4			
% egg	70.1	55.6		66.0	59.0	57.0	52.0	49.8	50.5			
water (%)	89	88.8		81	88	87.8	86.5	86.6	86.8			
lipid (%)	1	0		0	0	0.03	0.03	0.03	0.08			
protein (%)	10	11.1		17	12	10.6	11.5	11.6	11.3			
carbohydrate (%)	—	—		—	—	0.7	1.3	1.0	1.0			

TABLE 9 (continued)

Species	Mourning		Brown		Guinea					
	Starling	Dove	Pigeon	Pelican	Chicken	Chicken	Turkey	Fowl	Duck	Goose
inorganic (%)	—	—		—	0.6		0.7	0.8	0.8	0.8
kcal ⁶	3.20	2.253		58.40	23.19		28.72	13.10	26.10	70.78
kcal/g	0.63	0.63		0.96	0.68		0.65	0.66	0.65	0.64
Yolk lipid/protein	1.17	1.30	2.40	2.13	2.00		2.48	2.06	1.99	2.00
Yolk/white (wet)	0.24	.528		0.40	0.51		0.62	0.65	0.65	0.61
Yolk/white (dry)	0.94	1.827		0.71	2.16		2.37	2.48	2.71	2.58
Yolk/white (kcal)	1.33	2.524		1.16	3.14		3.89	4.01	4.36	4.19
Total lipid (g)	0.37	.418		5.54	5.92		9.11	4.30	9.25	24.04
(kcal)	3.54	3.971		52.66	56.20		86.55	40.81	87.92	228.87
Total protein (g)	0.69	.713		12.99	7.06		9.55	4.39	9.20	24.48
Total protein (kcal)	3.90	4.028		73.38	39.90		53.95	24.79	51.99	138.29
Total energy (kcal)	7.44	7.999		126.04	96.10		140.50	65.60	139.91	367.17
Kcal/g fresh egg weight	1.03	1.247		1.37	1.66		1.65	1.64	1.75	1.84
Protein/kcal	.093	.089		.103	.073		.068	.067	.066	.067

¹Ricklefs, unpublished.
²Spohn and Riddle, 1916.
³Lawrence and Shreiber, 1973.
⁴Brody, 1945.
⁵Romanoff and Romanoff, 1949.
⁶All caloric values are based on protein and lipid only with caloric values of 5.65 and 9.5 kcal/g, respectively.

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This amounts to 20-25% of the total energy in an egg for precocial species, and 40-50% for altricial species.

On the other hand, yolk material is secreted into several developing ova simultaneously by their follicle cells. Follicular growth rate is commonly estimated by measuring the follicles of a female collected just before she begins to lay. The progression of follicle sizes is assumed to represent the daily increment of growth. Measurements of follicle size, either as weights or as volumes calculated from diameters (assuming spherical shape), are presented in Figure 2 for the California

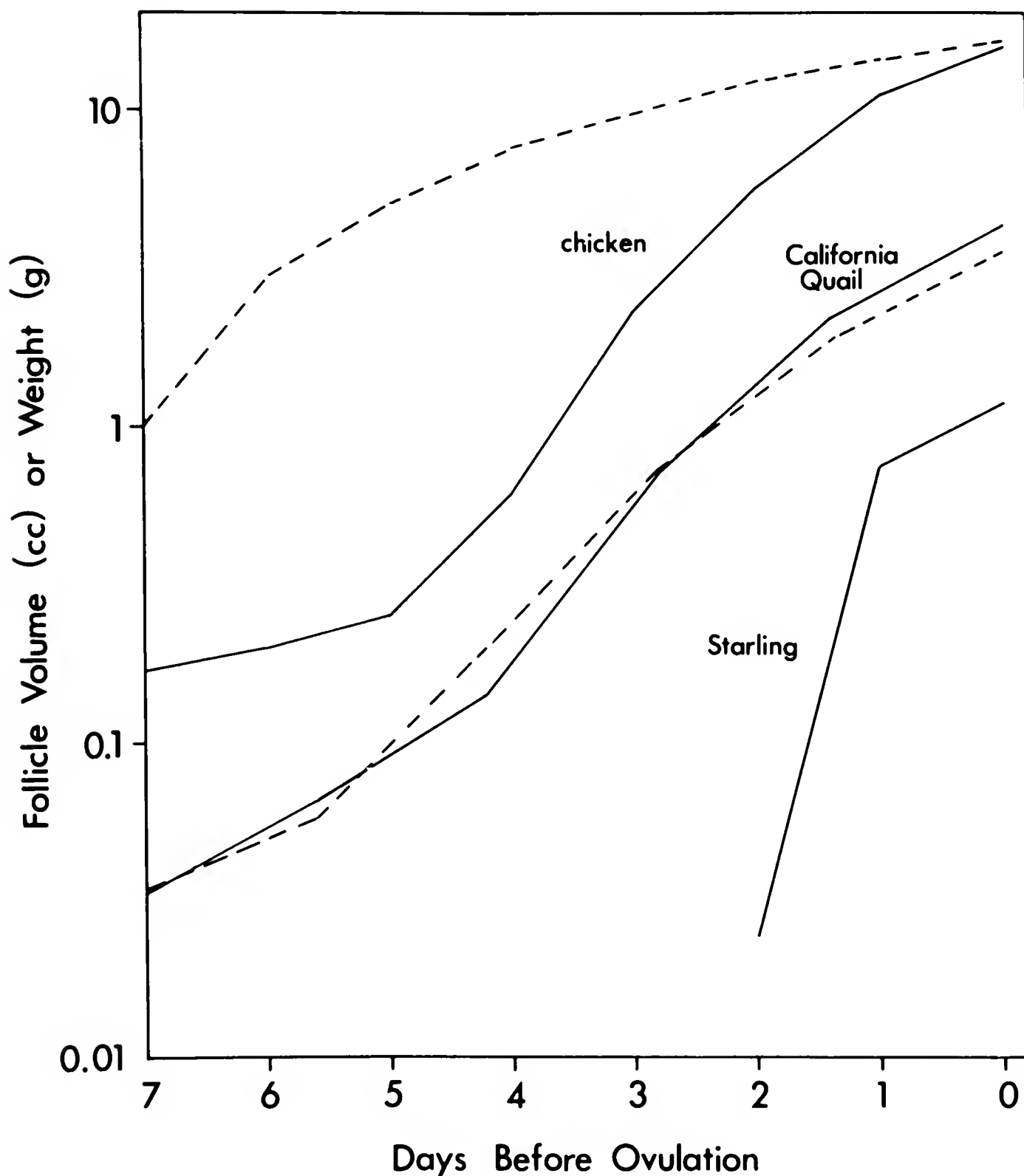


FIG. 2. Follicular growth in several species of birds. Domestic chicken: dashed line represents weight based on thickness of successive layers of yolk marked by dye (Warren and Conrad, 1939); solid line represents weight of successive follicles (Romanoff, 1931). California Quail: volumes calculated from diameters of successive follicles (solid line, Anthony, 1970; dashed line, Lewin, 1963). Starling: weight of successive follicles (Ricklefs, unpubl.).

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Quail, the domestic chicken, and the European Starling. A period of rapid growth begins 3 to 10 days before ovulation, depending on the eventual size of the egg (Fig. 3). Growth rate may be taken as equiva-

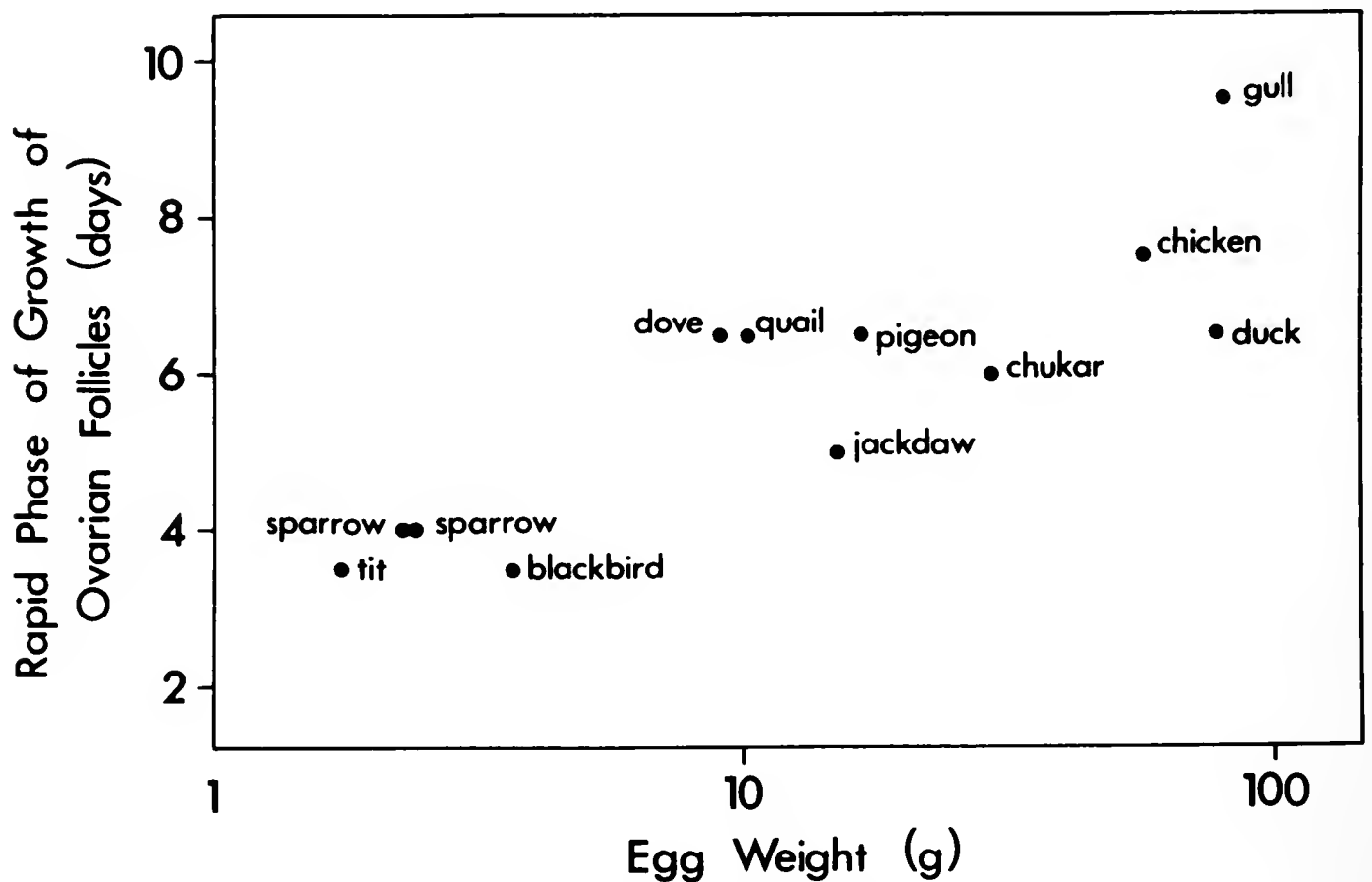


FIG. 3. Relationship of the length of the rapid phase of ovarian growth to egg weight (based on data compiled by King, 1973). These data are only approximate since the period of rapid growth is difficult to define and since some values are estimates. For example, Nice's (1937) estimate of four days for the Song Sparrow is based on the fact that a female can begin to replace a clutch within five days of a nest failure.

lent to the increment of energy content of the egg for only the last 3 or 4 days of follicular growth in precocial species. Smaller ova contain a greater proportion of water (80-85% compared to 45-50% for mature ova; Romanoff, 1943).

Ova of the duck, chicken, pheasant, and quail have similar growth rates when corrected for final weight. Romanoff (1943) showed that the percentage of final weight achieved prior to ovulation can be described approximately by the formula $\% = 26 - 4x$, where x is days before ovulation. During the week before ovulation the ovum increases by 2, 6, 10, 14, 18, 22, and 26% of its final weight on successive days.

It is tempting to derive a general model for follicular growth. If the rate of yolk formation is a function of the layer of follicle cells surrounding the ovum, the diameter of the ovum should increase by a constant amount each day and the volume should increase in proportion to the surface area of the ovum. Riddle (1911) found by giving daily injections of Sudan III, a fat soluble dye that colors thin layers of yolk and delimits daily increments of growth, that the radius of the domestic hen's egg increased at a constant rate of 2 mm per 24 hours during the rapid phase of growth prior to ovulation. But the slope

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of the relationship between the logarithm of the daily growth increment and the logarithm of follicle weight for Romanoff's (1943) data is 0.50 ± 0.10 . Hence the daily increment of follicle diameter increases as the $1/2$ power of its weight or volume, not the $2/3$ power of weight (that is, proportional to its surface area) as we would have predicted.

In species with short periods of rapid follicular growth, growth rate is correspondingly high. For example, the daily increment of weight in the ovum of the Starling, calculated from successive follicle sizes during the early part of the egg laying period, is 0.32 g between follicles I and II and 0.81 g between follicles II and III (Ricklefs, unpubl.). A freshly laid Starling egg contains 1.22 g of yolk and thus most of the growth of the ovum is completed in two days (see Fig. 2).

The actual growth rate of an individual follicle may be misrepresented by analysis of follicle sizes from a single ovary prior to ovulation of the first follicle. Warren and Conrad (1939) attempted to measure the growth of the White Leghorn hen's ovum during the final rapid phase of growth by injecting hens daily with Sudan III dye. The resulting weight growth curve, calculated from the radius of successive spheres delineated by layers of dye, differs considerably from growth curves based on sizes of successive follicles (Fig. 2). Warren and Conrad's data suggest that the first ovum of a clutch has a more prolonged period of growth than subsequent ova. Bissonette and Zujko (1936) have shown this to be the case in Starlings, but differences in development period between successive ova are not nearly great enough to reconcile the discrepancies created by Warren and Conrad's data. For the present, I shall assume that measurements of successive follicles just prior to ovulating the first ovum represent the true growth rate of ova. Any error resulting from this assumption will be on the side of higher growth rate.

CLUTCH SIZE, LAYING INTERVAL, AND MAXIMUM ENERGY REQUIREMENTS OF EGG FORMATION

If we know the follicular growth accomplished each day, the laying intervals between eggs, the number of eggs laid, and the energy contents of the yolk and white, we can calculate the maximum energy requirement of forming the clutch, as shown in Table 10 and Figure 4. The percent of growth accomplished per day is estimated from Romanoff's (1943) data; clutch size is assumed to be equal to the period of rapid growth in days, one egg is formed each day. Under these conditions the maximum rate for which energy is required for egg formation is equal to the energy content of a single egg. This level of requirement is reached whenever eggs are laid on a daily basis and clutch size is equal to or greater than the period of rapid follicular growth (see King, 1973).

If the laying interval is increased to two days, the daily energy requirement of ovum formation is decreased to about one-half (48 and 57% of the energy content of an ovum on the two days preceding each

TABLE 10
A Model of the Energy Requirement of Ova Formation in a Species that Lays a Clutch of 10 Eggs Over a 10-day Period.

Days before ovulation	% of final weight added per day ¹	Days before ovulation ²										Days after clutch initiation									
		10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	
1	26										X	X	X	X	X	X	X	X	X	X	
2	22										X	X	X	X	X	X	X	X	X	X	
3	18										X	X	X	X	X	X	X	X			
4	14										X	X	X	X	X	X	X				
5	10										X	X	X	X	X	X					
6	6										X	X	X	X	X	X					
7	2										X	X	X	X	X						
8	(1)										X	X	X	X							
9	(0.5)										X	X	X	X	X						
10	(0.5)										X	X	X	X	X						
Total ³	100.0	0.5	1	2	4	10	20	34	52	74	100	99.5	99	98	96	90	80	66	48	26	

¹Growth rate derived from a figure in Romanoff (1943; see text) with estimated values for days 8-10.

²The growth of an individual ovum can be traced on a diagonal up and to the right.

³Sum of growth increments for all follicles developing on a particular day.

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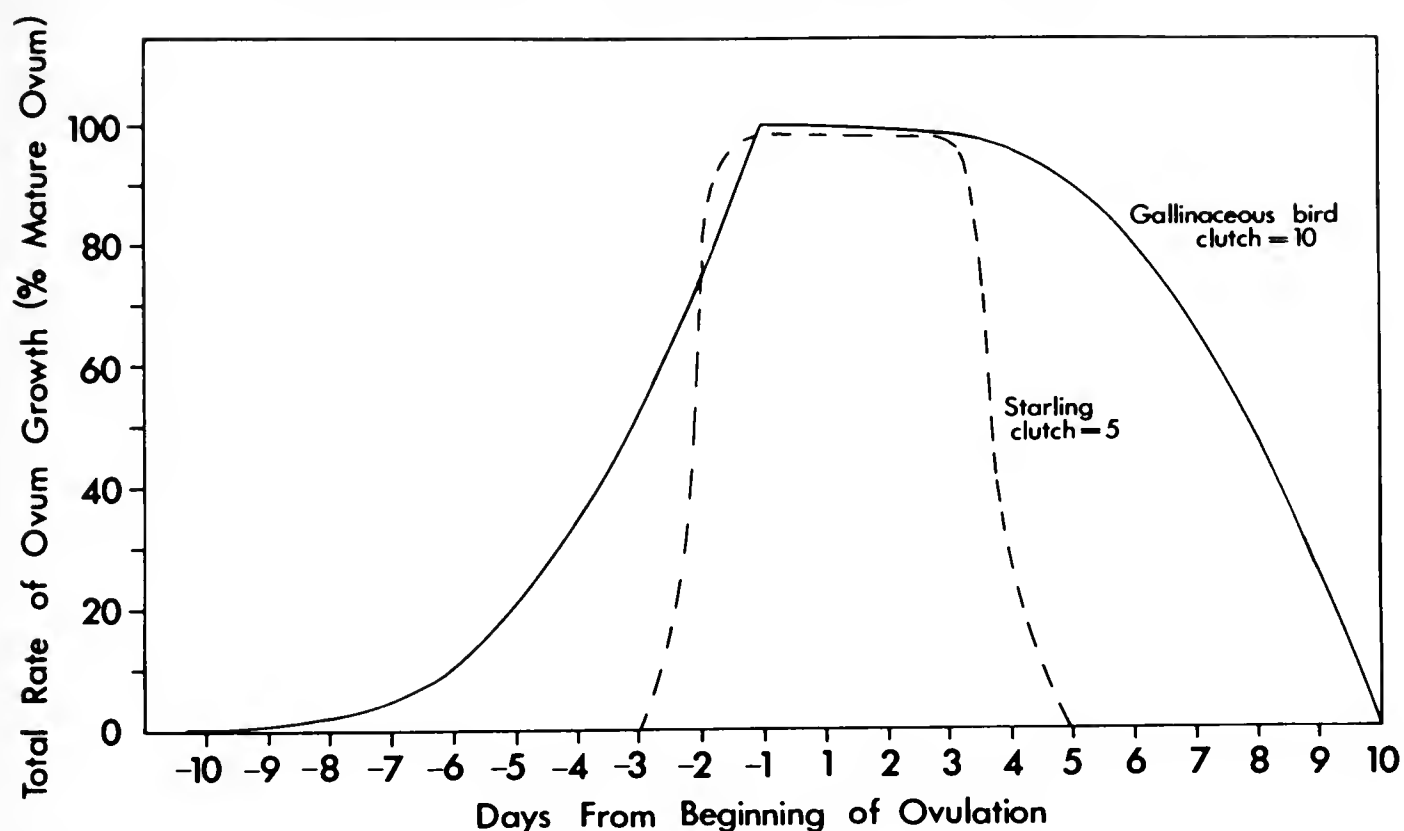


FIG. 4. Combined growth rate of developing ova, expressed as a percent of the weight of a mature ovum. Curves are presented for a gallinaceous bird with a 10-egg clutch (based on Table 10) and for the Starling (5-egg clutch), calculated in a similar manner, from data in Fig. 3.

ovulation). If the laying interval is increased to three days, the requirement is reduced to an average of one-third, with values of 25, 33 and 42% for the third, second, and first day prior to ovulation. Thus increasing the laying interval reduces the average maximum daily requirement as the inverse of laying interval, but the maximum daily requirement is 100, 57, 42, 36, 32, 28, and 27% of the energy content of a single ovum for intervals of one to 7 days.

If clutch-size is less than the number of days of rapid follicular development, the energy requirement for egg formation is also reduced. From the model presented in Table 10, maximum daily energy requirement for yolk formation in clutches from one to 10 is 26, 48, 66, 80, 90, 96, 98, 99, 99.5, and 99.75%, respectively, of the energy content of a single egg. Clutches greater than about 5 eggs apparently place little additional daily energetic burden on the female.

King (1973) estimated the daily energy requirement of egg laying in several groups of birds from egg weight, interval of laying, and energy content of the clutch. His values, expressed as percentages of basal metabolic rate, were 45-58% for three species of altricial land birds, 71-113% for seven galliform species, and 156-239% for four anseriform species. Egg laying evidently places a tremendous energetic strain on the female.

The size, number, and energy content of eggs varies considerably between species. If the rate at which birds can produce yolk material is limited, we should find compensatory adjustments in laying interval and period of rapid follicular development. The size and energy content of eggs in six groups of birds are presented in Tables 11 and 12.

TABLE 11
Relationship Between Egg Size and Body Size in Several Groups of Birds Fitted to the Model $Egg\ Weight = aW^b$ (data from various sources).

Group	n	Geometric mean		Egg weight (% adult)	Regression constants		
		Body weight(g)	Egg weight(g)		r	a	b
Passerines	25	25.2	2.59	10.3	.98	.24	.733
Galliformes	11	273.1	16.14	5.9	.62	1.70	.401
Hawks and Owls	15	502.2	32.83	6.5	.93	.84	.588
Ducks	5	947.0	53.40	5.6	.98	.64	.643
Shorebirds	13	77.0	13.21	17.2	.92	.90	.618
Gulls and Terns	11	220.5	34.44	15.6	.99	.95	.666

¹ s_b = standard error of regression slope, b .

TABLE 12
Energy Requirements of Egg Laying in Several Groups of Birds.

Group	Energy content of egg		Period of rapid growth (days) ³	Laying interval (days) ⁴	Typical clutch size	Correction factor ⁵	Energy requirement of laying (% BMR)
	(kcal/g) ¹	kcal					
Passerines	1.05	2.72	4	1	4-5	100	45
Galliformes	1.65	27.1	6	1	10-12	100	126
Hawks and Owls	1.05	34.5	7	3	2-4	38	39
Ducks	1.8	96.1	7	1	10-12	100	180
Shorebirds	1.7	22.5	6	2	4	56	149
Gulls and Terns	1.7	58.6	7	2	3	53	170

¹From Table 9 and text; percentage of yolk in eggs of hawks and owls is similar to that in passerine eggs (Nice, 1962) and thus energy contents are assumed to be similar.

²Energy content of egg multiplied by 1.33 to include energy of synthesis; BMR from appropriate equations for resting birds in Aschoff and Pohl (1970).

³Estimated from Figure 3.

⁴From Lack (1968a).

⁵Maximum percent of energy content of one egg produced each day. Value of egg white is also included. The white of one egg contains 45% of the energy in eggs of altricial land birds and 25% of the energy in eggs of precocial species.

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The energy content of the egg, expressed as a percent of BMR, is lowest for passerines (45%), intermediate for raptors (103%) and galliforms (126%), and highest for ducks (180%), shorebirds (226%), and gulls and terns (320%). To calculate the energy requirement of egg formation, these values must be adjusted for clutch-size, laying interval, and period of rapid follicular development. The energy requirement for laying in passerines is probably equal to the energy content of each egg because the laying interval is usually one day, and the period of rapid follicular development is similar to the clutch size (about 3 to 5). This applies to galliformes and anseriformes as well. In raptors and shorebirds the energy requirement of laying is less than the energy content of the one egg because clutch size is small and the laying period is prolonged. Periods of rapid follicular development increase with egg size as one would expect (Fig. 3). If we assume that the percent of final ovum weight achieved each day increases linearly during the period of follicular growth, we can calculate the maximum daily growth increment of the follicle and the amount by which the growth increment increases each day (Table 13). We can now calculate

TABLE 13

Maximum Daily Increment of Growth of the Ovum, Expressed as a Percent of its Final Energy Content, and the Daily Increase in the Growth Increment; Both are Related to the Period of Rapid Follicular Development.

	Length of development period (days)									
	1	2	3	4	5	6	7	8	9	10
Maximum increment ¹	100	67	50	40	33	29	25	22	20	18
Daily increase ²	100	33	16.7	10	6.7	4.8	3.6	2.8	2.2	1.8

¹General formula is $2/(n+1)$ where n = number of days.

²General formula is $2/n(n+1)$.

the average energy requirement for follicle growth, expressed as a percent of the energy requirement of a single egg (prorating the synthesis of albumen over the laying interval). For hawks and owls this requirement (the correction factor of Table 12) is 38%; for shorebirds and for gulls and terns, it is 56 and 53%, respectively. The resulting energy requirement for egg production is about 40-50% BMR for species with altricial young and 125-180% BMR for species with precocial young.

These values for energy requirements for egg production were calculated on the basis of data for birds with average body weight. But the size of eggs relative to body weight varies with adult body weight

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(Table 11). In passerines the power of the egg size-body size relationship is 0.733 ± 0.047 (SE), which is nearly identical to the relationship of standard metabolism to body weight (Table 4). Therefore, all other factors being equal, the energetic cost of egg production relative to BMR in passerine birds does not change with body weight. In other groups, the slope of the egg size-body weight relationship (0.40-0.67) is less than that of the metabolism-body weight relationship, so egg production potentially creates a more severe energetic strain on smaller species. Rapid follicular development further enhances this problem in small species. Small birds may compensate by extending the laying interval, but I have not sought data to test this point.

Several species demonstrate how the energy requirements of egg formation may be reduced. For their adult body size, megapodes lay enormous eggs (Lack, 1968a) which contain more than 60% yolk (Nice, 1962). The approximately 200-gram egg of a 2,000-gram megapode would contain about 532 kcals and require 708 kcal for its production, or about 577% of BMR (I assumed 0.65 kcal/g albumen and 4.0 kcal/g yolk). The laying interval of megapodes is 5 days, however. If we assume that rapid follicular growth requires nine days, the energetic requirement of egg production is only 28% of the energy value of a single egg (20% yolk energy plus 100% white energy) or 162% BMR. This value is well within the range of other precocial species.

Some tropical passerines skip days between laying successive eggs, thereby reducing the energy requirement of laying even though birds with altricial young expend relatively little energy on egg formation regardless of the laying interval. The Black-and-White Manakin (*Manacus manacus*) lays two large eggs (16% of body weight compared to 11% for most passerines), and lays only every other day. Spacing of eggs may be necessary for accumulation of sufficient protein by this frugivorous species, but this problem will be dealt with in detail below. I have examined many of the life history studies of Skutch (1954, 1960, 1969) for possible correlations between extended laying intervals and diet, ecology, and body size in tropical passerines weighing between 6 and 50 grams. Most of the suboscines examined (23 species of Tyrannidae, 4 Pipridae, and 5 Formicariidae) had laying intervals of two days, but none of the oscines (2 Hirundinidae, 10 Thraupidae, and 7 Fringillidae) had laying intervals greater than one day. This strict taxonomic distinction is paralleled by differences in egg size between the two groups. The relationship between egg volume (cc) and adult female body weight (g) is expressed by the equation

$$\text{egg volume} = 0.316 W^{-0.293}$$

for 21 species of suboscines (correlation coefficient $r = -0.70$ and $s_b = 0.021$), and

$$\text{egg volume} = 0.167 W^{-0.111}$$

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for 17 species of oscines ($r = -0.40$ and $s_b = 0.014$). The corresponding equation for 19 species of temperate passerine is

$$\text{egg volume} = 0.237 W^{-0.242}$$

($r = -0.77$ and $s_b = 0.017$). These egg size-body weight relationships demonstrate that the eggs of suboscines are substantially larger than those of oscines (24% larger for species weighing 10 g, 10% larger for species weighing 20 g). Larger egg size may be the primary reason for extended laying intervals in small suboscines but would not explain this phenomenon in species weighing more than 20 g. (One is tempted to speculate that large egg size suggests a primarily tropical origin for most suboscines and that small egg size indicates a primarily temperate origin, associated with large clutch-size, for oscine families in the New World.)

Birds may also extend the period of follicular growth to reduce the energy requirements of producing the clutch, particularly if few eggs are laid. The Herring Gull has a long period of follicular development for the size of its egg (9-10 days; King, 1973). Further comparative data on the growth of the ovum would be interesting.

Availability of energy potentially limits the rate of egg formation, but the availability of protein and of minerals for shell formation may also be critical. Ratios of protein to kcals (g/kcal) in the eggs of altricial species were 0.089, 0.093 and 0.103, and for precocial species 0.066 to 0.073 (Table 9). If we assume a production efficiency of 75%, reasonable estimates of protein/kcal ratios are 0.073 and 0.051, respectively. Such protein levels are easily supplied by diets of flesh, fish, and insects, but fruits and grains, with ratios of 0.011 to 0.029 (Table 2), may not be adequate. For example, consider a 25 gram passerine bird that lays a 2.6 gram egg with a caloric value of 1.10 kcals/g, a protein/kcal ratio for its production of 0.075, and a maximum daily energy requirement for egg formation of 45% BMR. If the bird's daily metabolic rate during the egg laying period is 3 times BMR, egg formation will require 15% BMR and a protein/kcal ratio for egg formation of $0.15 \times 0.075 = 0.013$. This requirement is slightly greater than the protein supplied by tropical fruits (Table 2). A reduction of adult metabolism or increase in egg size in a tropical frugivore would require prolongation of follicular growth or an increase in the interval between eggs, as in the Black-and-White Manakin, (see above). If a particular time during the daily cycle is optimum for egg laying, laying intervals will be increased by whole days. In fact, most passerine birds lay their eggs in the early morning (Skutch, 1954, 1960, 1969) perhaps to avoid the presence of an egg with shell in the oviduct during the daily activity period.

Egg shells account for about 7% of the fresh weight of eggs in altricial species and 11% in precocial species (Table 8). Shell formation, therefore, requires about 0.05 g mineral ash per kcal for both altricial and precocial species. Digestible components of most food

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items listed in Table 2 contain 0.005 to 0.02 g mineral ash/kcal (Watt and Merrill, 1963) which is barely adequate for egg formation when the energy requirement of egg formation is 15% of existence metabolism, as in the example presented above. Of course, the elemental composition of mineral ash in most foods, which contain primarily potassium, sodium, and phosphorous, does not match that in eggshell, 98% of which is calcium carbonate (Romanoff and Romanoff, 1949). Thus the overall mineral ash requirement is greater than I have suggested above. Because at least some species operate demonstrably close to the availability of protein and minerals in their normal diets, we may expect these factors to be limiting in some cases (see, for example, West and Norton, MS). Our preoccupation with energy has limited our investigation of these nutritional requirements in natural populations, an oversight that must be remedied.

EFFECT OF EGG LAYING ON ADULT PHYSIOLOGY

Egg production is a major energetic event in the reproductive cycle of the female, and we could, therefore, expect correspondingly marked changes in physiology prior to and during the egg laying period. Changes in blood composition usually parallel increased requirements of nutrients for egg formation. Blood lipid levels rise with egg formation by 35% in the pigeon (Riddle, 1927), about 50% in the domestic fowl (Lawrence and Riddle, 1916), and 500-600% in the pheasant (Breitenbach, et al., 1963) and dove (Riddle, 1942). Part of this increase may be related to fat deposition and other concurrent events. Blood calcium increases by 100% in the pigeon prior to ovulation (Riddle, 1927). This change may increase the permeability of follicular membranes, thereby aiding transport of substances into the developing ovum, as well as providing calcium for shell formation. Blood sugar increases by 20% during ovulation in the pigeon (Riddle and Honeywell, 1923). On the other hand, blood sugar levels in the Bank Swallow (*Riparia riparia*) during the egg laying and nestling periods were similar, but this level was less than half that during the burrowing and nest-building period (Petersen, 1955). Petersen (1955) suggested that blood sugar was correlated with activity level during the reproductive cycle, but the absence of information on metabolic rates of free-living birds prevents us from drawing firm conclusions from his study.

Females of many species gain weight prior to egg laying and then lose much of it during the laying period. (Ring-necked Pheasant, Breitenbach and Mayer, 1959; California Quail, Anthony, 1970; Gambel Quail (*Lophortyx gambelii*), Raitt and Ohmart, 1966; Bank Swallow, Petersen, 1955). Growth and atrophy of the ovary and oviduct accounts for much of the change. Increases in body fat and in the weight of the intestines and liver are important in pheasants. Increase in body water also may be a general feature of preovulatory weight gain (e.g., Brisbin, 1969). The decrease in weight during and just after

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egg laying, which may amount to 10-20% of body weight, need not imply an energetic drain on the female because weight usually returns to normal nonreproductive levels. Weight losses may indicate nothing more than the dismantling of the egg producing machinery. The problem of weight change will be considered in more detail later.

Metabolic energy intake during laying and nonlaying has been measured for domestic hens (Brody, 1945) and captive pheasants (Breitenbach, et al., 1963). Recorded increments for egg laying in these species, 62% and 65% respectively (King, 1973), are about one-half the expected percentages of BMR calculated in Table 12, suggesting that maintenance metabolic levels are about twice BMR. In chickens the ratio of maintenance to basal metabolism is actually 1.7 (Brody, 1945). King (1973) suggested that free-living birds function at 3 to 4 times the basal level of energy expenditure and estimated that the daily maximum cost of egg production is 21-30% of the daily energy intake in galliform birds (assuming constant body weight), 52-70% in ducks and geese, and 13-16% in passerines. Similar estimates based on Table 12 would not differ much from King's values.

ENERGY DEPRIVATION AND EGG PRODUCTION

Because egg production forms a large part of the energy budget of the female, one would expect energy deprivation to have an adverse effect on egg laying performance. The process of egg formation itself is energetically conservative; deprivation does not alter the size and quality of eggs appreciably, only their number. Restriction of diet to 87.5% and 75% of *ad libitum* levels in White Leghorn hens reduced egg production to 66-69% and 46-47% of controls, respectively, but body weight was not affected (Heywang, 1940). Similar results have been reported by Milby and Sherwood (1956), and by Singsen, et al. (1954). Walter and Aitken (1961) point out that normal egg production rates are resumed after feeding restrictions are removed. Restriction of diet to 61% of *ad libitum* maintenance levels had no effect on egg production in Bronze Turkeys although the hatching rate of fertile eggs decreased from 65% in the controls to 54% (Scott and Payne, 1941). Brietenbach, et al. (1963) observed egg production of pheasants of 9% of normal rates with restriction to 72% of the *ad libitum* rate during the laying period. Weight gain of the adult pheasants was curtailed by dietary restriction (although gonad, and oviduct and visceral organ weights were near normal) and fat levels were also greatly reduced. The effects of dietary restrictions on egg production in these experiments are consistent with King's estimate that egg production should require 21-30% of the energy intake of free-living galliform birds.

ENERGETICS OF INCUBATION

Birds must maintain the temperature of their eggs close to that of their bodies to ensure normal and rapid development of the embryo.

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To maintain high and constant incubation temperatures the adult must replace heat lost from the eggs to the environment with heat from its own body. (In exceptionally hot climates birds occasionally have to remove heat from their eggs to keep egg temperature within the optimum range.) Because birds have many adaptations that reduce heat loss from the eggs and facilitate heat transfer between the adult and the eggs, incubation must be an important part of the energy budget of the reproductive cycle. In spite of this, the energetics of incubation are not well understood. In this section we shall examine the physical environment of the eggs, the temperature of incubation, estimates of the energy requirements of incubation, the sources of heat for incubation, and aspects of the parental strategy of incubation rhythm. During this discussion we must keep in mind that incubation patterns are constrained by external considerations as well. For example, nest structure can be limited by the availability of nest sites, building material, and predator pressure. Incubation rhythm and constancy are controlled to some extent by adult foraging requirements. Above all, we must ask whether the requirements of incubation can limit the ultimate production of young, particularly by restricting clutch size.

PHYSICAL ENVIRONMENT OF THE EGG: THE NEST

Nest structure varies widely among birds. The form of the nest must balance the need for heat conservation (and perhaps shading) during the incubation and nestling periods, the possible need for heat dissipation from broods of large young in warm climates, and the need to escape detection by predators. Nests in inaccessible positions, as at the ends of branches, can be bulky and conspicuous, with good insulation, but not be subjected to increased predation. Nests placed in more abundant, but more accessible, sites may have poorer thermal properties because of the need to reduce bulk for the sake of concealment.

Nests of precocial birds, whose young leave the nest after hatching, are perhaps more indicative of thermal relationships during incubation. Most of these nests are built on the ground and they vary from scrapes in the ground with no lining, as in many shorebirds, to the thickly down-lined nests of many ducks. In general, the larger the clutch the greater the insulative capacity of the nest. This trend also appears in altricial species that lay large clutches, such as bushtits, kinglets, and titmice (Riehm, 1970).

Thermal qualities of nests are poorly known. Palmgren and Palmgren (1939) measured the insulative value of the nests of several species by the rate at which a flask of water placed in the nest cooled. More accurate comparative measurements are needed, however, perhaps adapting Drent's (1970) method for measuring the loss of heat from an egg. Nonetheless, behavioral adaptations of nest placement and orientation (Horvath, 1964; Ricklefs and Hainsworth, 1969; and Austin,

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1974, *in press*) amply demonstrate the importance of thermal considerations to nest structure and placement, and point the way to a much neglected area of study.

PHYSICAL ENVIRONMENT OF THE EGG: THE BROOD PATCH

Heat lost from the eggs must be replaced by the incubating adult to maintain the proper temperature for embryonic development. Many species develop an "incubation patch" or "brood patch" over that portion of the body surface which directly contacts the eggs to open a gate of heat transfer between the body of the adult and the clutch (Tucker, 1943; Bailey, 1952; Jones, 1971).

The brood patch develops in ventral apteria by defeathering of any down and by increasing the vascularization, intercellular fluid, and number of cells in the epidermis and dermal connective tissue. Incubation patches occur in most orders of birds, but the Pelecaniformes, Anseriformes, many Columbiformes, and some of the Alcidae lack them (Jones, 1971). The apteria of doves are bare of down, so eggs contact the skin directly even though no specialized patch develops. The lack of brood patches in Columbiformes and Pelecaniformes may be related to their tropical distribution and small egg mass. Most species of Anatidae pluck the down from their ventral surfaces for nest lining, and thereby essentially bring the eggs within the body covering during incubation. Brood patch formation may be energetically impossible for many ducks and geese that spend a large portion of their time sitting on cold water.

Defeathering and histological changes in the brood patch region are usually completed in passerines by the time the clutch is completed. In galliformes, on the other hand, defeathering may not be completed until the middle of the incubation period and full histological development of the brood patch may not be attained until the eggs hatch. Refeathering occurs soon after hatching in precocial species, but is delayed in altricial species, which suggests that brooding by precocial species may function primarily to reduce heat loss from the young, and not to provide heat (Jones, 1971). Brood patch development itself probably does not place any energetic strain on the adult. In Bank Swallows, for example, the mature brood patch weighs about 300 mgm. Growth is accomplished at a rate of about 20 mgm per day, which is less than a tenth the combined growth rate of the ovary and oviduct (Petersen, 1955).

The special morphological properties of the brood patch do not raise the skin temperature, but bring heat to the skin at a rapid rate. Heat is transferred between adult and eggs at a rate proportional to the area of contact and to the temperature gradient between the skin and the eggs. The eggs must be cooler than the body of the adult for heat transfer to occur and, in fact, the eggs tend to cool the brood patch by drawing heat away. This cooling effect of the eggs, which reduces the skin-egg temperature gradient and thereby tends to reduce heat trans-

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fer, must be balanced by an increase in heat transfer to the brood patch. Heat flow is facilitated by increased blood flow through increased vascularization. The greater the heat loss from the eggs to the external environment, the greater the need for rapid heat flow to the brood patch. In the absence of a brood patch birds would either have to reduce incubation temperature, thereby increasing the skin-egg temperature gradient until a heat flow equilibrium is reached, or increase body temperature, also increasing the skin-egg gradient. Reducing incubation temperature would reduce embryonic growth rate; increasing body temperature, if physiologically feasible, would increase adult heat loss. Edema and hyperplasia of the skin thicken and soften the incubation patch region and thus allow the incubation patch to fit the contours of the eggs more closely. Increasing the area of skin-egg contact increases the rate of heat transfer.

TEMPERATURE OF INCUBATION

Before incubation patch formation skin temperatures on the surface of the ventrum are probably similar to body core temperatures. Surface temperatures of incubation patches are about a degree Celsius lower than body core temperature because heat is withdrawn by the eggs (see Table 14). Mean egg temperatures average 3.7°C below incubation patch temperatures with a range of 1.5-5.5°C, depending on the species. The largest gradients between incubation patch and clutch tempera-

TABLE 14

Temperature Characteristics of Incubation (from data compiled by Drent, 1970).¹

Property	Number of Species	Mean (°C)	SD (°C)	Maximum (°C)	Minimum (°C)
Body temperature	10	40.26	1.13	41.3	37.9
"	8 ²	40.71 ³	0.62	41.3	39.5
Brood patch temp.	8	39.70	0.96	40.7	37.8
Internal egg temp.	12	35.82	1.25	38.3	33.7
Egg-skin gradient	8	3.68	1.27	5.5	1.5
Skin-body core gradient	8	1.01	0.61	1.9	0.3
Egg-body core gradient	10	4.42	1.34	1.9	2.8

¹Including only species in which egg temperature was measured by telemetry and in which body temperature data were available.

²Those species for which brood patch skin temperature was available.

³Significantly different from brood patch temperatures with > 95% confidence, $t = 2.51$.

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tures occur in species with large clutch masses (*Tyto alba* 5.1°C, *Troglodytes aedon* 5.5°C; Howell, 1964; Kendeigh, 1963; Baldwin and Kendeigh, 1932); the smallest gradients occur in species with relatively small clutch masses (*Puffinus pacificus* 1.5°C, *Larus argentatus* 2.2°C; Howell and Bartholomew, 1961 and Drent, 1970).

Normal egg temperatures during incubation vary between about 34 and 38°C (Drent, 1973). Many of Huggins' (1941) values, which average 34.0°C \pm 2.38 (SD) for 37 species in 11 orders, are apparently too low because Huggins did not record temperatures over a long enough period to obtain equilibrium values from undisturbed birds (Drent, 1973). Because the temperature of eggs drops when the parent is not incubating (see below), and because ambient temperature influences the rate of heat loss from eggs, egg temperature varies within narrow limits as a function of air temperature (cf. Kendeigh, 1963). This relationship is discussed by Kendeigh (1952, 1963) and Drent (1970, 1972, 1973) and will not be mentioned further here.

ENERGY REQUIREMENTS OF INCUBATION: KENDEIGH'S FORMULA

Indirect estimates of the energy required to maintain eggs within the normal range of incubation temperatures have been based on calculations of the rate at which a clutch of eggs loses heat. Direct measurements of the metabolism of incubating adults have proved to be technically difficult (see below).

Kendeigh (1963) pioneered the indirect estimation of the energy requirements of incubation by deriving a formula for the rate of heat loss from eggs. The equation has the form:

$$\text{kcal/day} = n \cdot w \cdot h \cdot b \cdot (t_e - t_{na}) \cdot i \cdot (1 - ca) / 1000$$

where

- n = number of eggs
- w = mean weight of eggs (g)
- h = specific heat of eggs (cal/g·°C)
- b = rate of cooling (°C/hr·Δtemp.)
- t_e = egg temperature (°C)
- t_{na} = nest air temperature (°C)
- i = interval in hrs (24 hrs if values are to be kcal/day)
- c = proportion of surface of eggs covered by incubating bird
- a = proportion of time bird is on the nest.

The constants of the equation, n , w , h , and b , transform data on temperature loss per unit time to heat loss per unit time and allow incubation requirements to be put on an energetic basis.

Most of the data required for the equation are measured directly at the nest (n , w , t_e , t_{na} and a). The area of the egg covered by the incubation patch does not contribute to the heat loss of the egg and is corrected for by the term $(1 - ca)$ in Kendeigh's equation. Kendeigh

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(1963) estimated the proportion of the egg covered by the incubation patch (*c*) to be 25% for the House Wren. Drent (1970) divided the surface area of the incubation patches of Herring Gulls by the total surface area of their eggs to obtain a value for *c* of 18%.

Specific heat of eggs (*h*) has been measured for the domestic fowl (0.772 cal/g·°C; Romanoff and Romanoff, 1949) and for the duck (0.80-0.78cal/g·°C, decreasing as incubation progresses; Kashkin, 1961). It is probably reasonable to adopt a value of 0.78 for most precocial species and 0.80 for most altricial species, whose eggs contain a greater proportion of water (see Table 9) with specific heat of 1.0 cal/g·°C.

Cooling rates (*b*) have been determined experimentally by measuring the drop in egg temperature when the egg is placed, fully exposed, in a chamber with a constant, low air temperature. Because heat loss is directly proportional to temperature gradient (*t_e - t_a*), the cooling rate is equal to the slope of the relationship of temperature drop per unit time (Δt) to egg temperature (*t_e*). The data presented in Table 15

TABLE 15
Hypothetical Temperatures, Measured over 12 Equal Time
Periods, of an Egg Initially 37° C Placed in a 15° C Chamber.

Time interval	Egg temperature (°C)		Midpoint temperature (°C) ¹		Temperature change (Δt)	Initial temperature gradient (<i>t_e - t_a</i>)
	Initial	Final	Arithmetic	Geometric		
1	37.0	33.2	35.1	35.05	3.8	22.0
2	33.2	30.2	31.7	31.66	3.0	18.2
3	30.2	27.8	29.0	28.98	2.4	15.2
4	27.8	25.8	26.8	26.78	2.0	12.8
5	25.8	24.3	25.05	25.04	1.5	10.8
6	24.3	23.0	23.65	23.64	1.3	9.3
7	23.0	22.0	22.50	22.49	1.0	8.0
8	22.0	21.2	21.60	21.60	0.8	7.0
9	21.2	20.6	20.90	20.90	0.6	6.2
10	20.6	20.1	20.35	20.35	0.5	5.6
11	20.1	19.7	19.90	19.90	0.4	5.1
12	19.7	19.4	19.55	19.55	0.3	4.7

¹Arithmetic midpoint is (*t₁ + t₂*)/2; geometric midpoint is exp [(log *t₁* + log *t₂*)/2].

represent the temperatures of a hypothetical egg, initially 37°C, placed in a 15°C chamber and measured over 12 equal time intervals. The temperature change during each interval is plotted as a function of the midpoint of temperature gradient during the interval in Figure 5. The slope of the relationship, 0.22 C/°C per unit of time, is the cooling constant *b*. In this contrived example, the rate of cooling falls to zero when the egg temperature is 3.1°C above the ambient tempera-

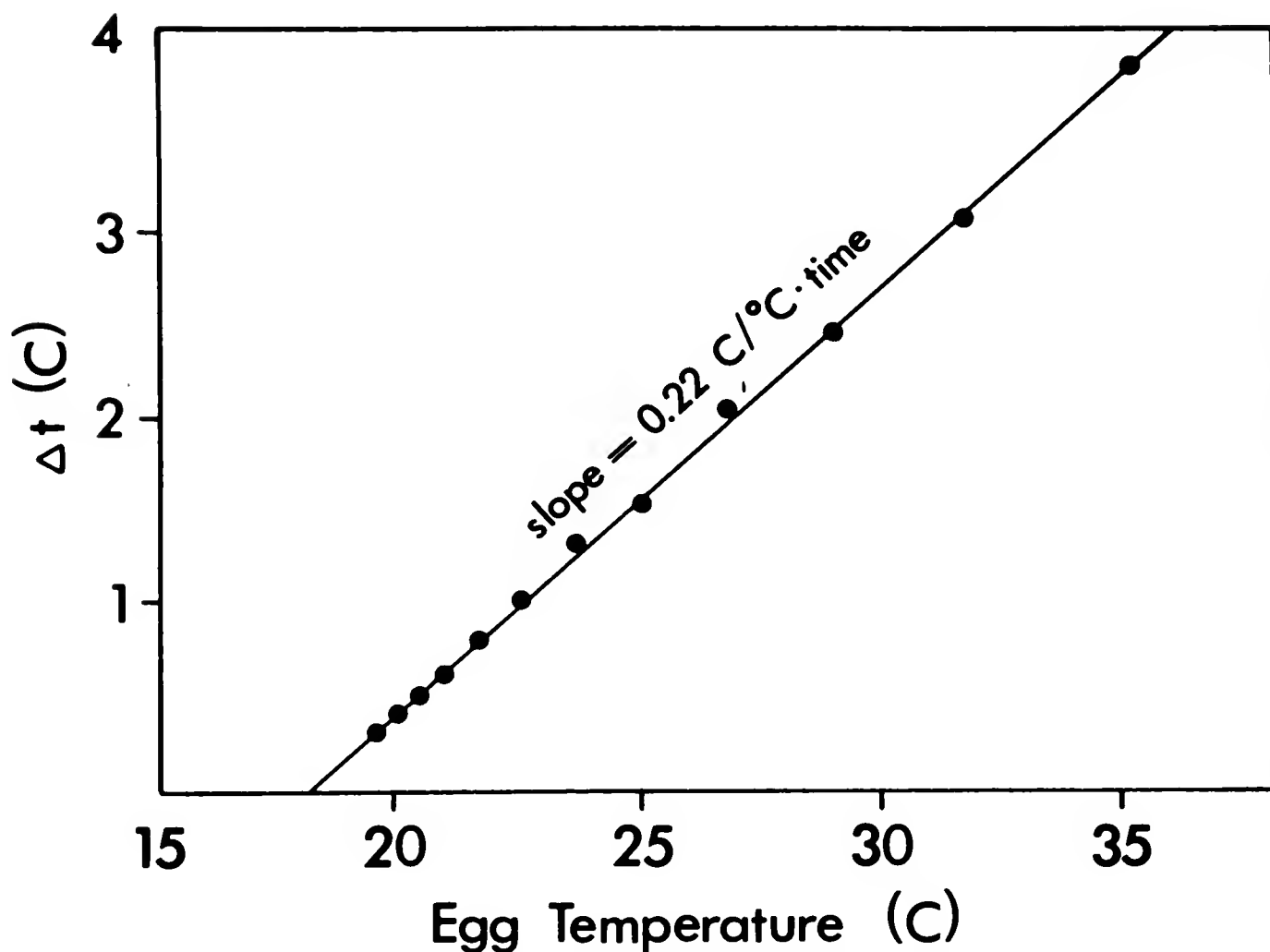


FIG. 5. Relationship between the temperature of an egg cooling in a constant temperature environment and its rate of cooling (based on data in Table 15). The slope of the relationship is the cooling constant of the egg, b .

ture. This situation is commonly encountered, particularly when measuring the cooling rates of young altricial birds, and indicates that metabolism balances heat loss at that temperature (see below).

If the loss of heat from an egg is directly proportional to the surface area, the cooling constant b should decrease as the cube root of egg weight. (The ratio of the heat dissipating surface to the heat containing volume is approximately the $\frac{2}{3}$ power of its weight divided by the first power of weight: $W^{2/3}/W^1 = W^{-1/3}$.) Kendeigh (1973) has summarized available data on cooling rates, which are presented in Table 16 with calculated values for conductance. If we eliminate the value for the Ruddy Duck (*Oxyura jamaicensis*) egg, which seems unusually high for its size, the regression of cooling rate on egg weight for the remaining 10 species is

$$\log b = \log 6.71 - 0.412 \log W \pm 0.124$$

and for conductance is

$$\log c = \log 5.35 - 0.418 \log W \pm 0.125$$

where W is egg weight in grams. The slope of either regression is not significantly different from -0.33 with the present sample, but the slopes more closely resemble the regression of conductance on body weight in dead, defeathered birds (slope = -0.44 , see Table 4). Deviation of the slope of the conductance-egg weight relationship from

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TABLE 16

Cooling Constants as a Function of Egg Size in Birds (after Kendeigh, 1973)¹

Species	Egg weight (g)	Cooling rate (°C/°C · hr)	Conductance (cal/g · hr · °C) ²
Graylag Goose	180	0.73	0.57
Herring Gull	94	1.09	0.85
Domestic Duck	78	1.16	0.90
Ruddy Duck	66	2.46	1.92
Jungle Fowl	53	1.21	0.94
Pectoral Sandpiper	11.8	2.50	1.95
Dunlin	11.2	2.56	2.00
Baird's Sandpiper	9.0	2.90	2.26
House Wren	1.4	5.20	4.16
Blue Tit	1.2	7.55	6.04
Zebra Finch	0.98	5.87	4.70

¹Original data from Kendeigh (1963), Kashkin (1961), Drent (1970), Norton (1973), and unpublished data of R. Drent, W.R. Siegfried, and J.A.L. Mertens.

²Cooling rate × 0.78 or × 0.80 for nonpasserines and passerines, respectively.

−0.33 could be caused either by the insulative properties of the egg itself or by the fact that large eggs tend to have thicker shells, or both (log thickness (mm) = log 0.102 + 0.291 log weight (g) ± 0.036 for 10 species; Asmundson, et al., 1943).

Evaporation of water from the egg constitutes another avenue of heat loss in addition to conduction of heat to the air and radiation of heat to the surroundings (see Kashkin, 1961). Drent (1970) compiled data from many sources for weight (= water) loss per day as a function of egg weight (range 1.46-169.6 g). The regression equation for 57 species has the form

$$\text{weight loss (g/day)} = 0.0151 W (g)^{0.741}$$

Since the surface area of an egg may be estimated by the function

$$\text{surface area (cm}^2\text{)} = 4.558 W (g)^{2/3}$$

(Romanoff and Romanoff, 1949:110), weight loss per unit of surface area is described by the relation

$$\text{weight loss (g/cm}^2 \text{ day)} = 0.00279 S^{1.112}$$

Because the slope of this regression is slightly greater than 1, large eggs must be relatively more porous than small eggs.

The daily weight loss of a Herring Gull egg (0.45 g/day) corresponds

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to a heat loss of 12 cal/hr (the heat equivalent of evaporation is 580 cal/g at 30°C), which is insignificant compared to the energy requirement of incubation of 200-400 cal/egg/hr (Drent 1970). Similar values for evaporative water loss have been reported for the fowl (15-20 cal/egg/hr; Romijn and Lokhorst, 1956) and the duck (7.5 cal/egg/hr; Khaskin, 1961). These data suggest that evaporation is generally a negligible component of heat loss from the egg.

Having determined values for all the parameters in Kendeigh's equation, one can readily calculate the rate of heat loss of the eggs. Kendeigh found that for the House Wren, egg temperature varied narrowly between 34.7 and 35.0°C, and nest air temperature (obtained in nest lining just under eggs) varied from about 31 to 35°C over an ambient temperature range of 20 to 32°C. Only the female incubates, and she covers the eggs about 75% of the 24 hr day. With these values, and others presented above, Kendeigh (1963) calculated that, depending on environmental conditions, between 1.1 and 2.6 kcal of heat must be supplied to the clutch each day to maintain their temperature. The energy requirement of incubation increases with decreasing ambient temperature and it is higher for nest boxes placed in the shade than in the full sun. El-Wailley (1966) estimated that the energy requirement of incubation in the Zebra Finch varied from 0.08 kcal/pair per day at 34.4°C to 4.78 kcal/pair per day at 14.5°C; incubation was not successful at the lower temperature.

Drent (1970) has found Kendeigh's formula accurate for the particular circumstances specified by the constants by an elegant measurement of the heat that must be added to a Herring Gull egg from an artificial brood patch to maintain a constant temperature in the egg. In a later paper, Drent (1972) summarized available data on the heat requirement of incubation for several species calculated by Kendeigh's formula (Table 17). Most of these values fall within the range of 15-25% of productive energy. When these estimates are recalculated as a percent of BMR, they are similar to estimated requirements for egg production (Table 12) in small passerines and the Dunlin, but relatively low for the Herring Gull. King (1973) also recalculated these data, perhaps more meaningfully, as a percent of the resting metabolic rate of the incubating bird at the temperature in question. For Zebra Finches King estimated the incubation requirement as 11 to 22% of adult metabolism at 29.1 to 14.5°C; House Wren 22% at 17°C to 10% at 22°C; Herring Gull a maximum of 32% of adult metabolism.

Although Kendeigh's equation has no inherent flaws, its application to incubation energetics may be misleading. In particular, by estimating cooling rates of eggs from measurements of the temperature of individual eggs in the laboratory, and by failing to consider the loss of heat from the nest itself, we ignore natural characteristics of incubation. In fact, resulting errors are small and tend to cancel each other. Therefore, Kendeigh's equation can yield essentially correct results even as it is currently used.

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TABLE 17

Heat Requirement for Incubation Estimated by Kendeigh's Formula
(based on Drent, 1972).⁶

Species	Weight (g)		Heat require- ment (kcal/ parent · day)	PE ¹ (kcal/bird · day)	BMR ²	Heat requirement	
	Adult	Clutch				%PE	%BMR
House Wren	10	8.2	1.6 ³	8.3	4.05	19 ⁴	40
Zebra Finch	12.1	3.8	1.5 ⁷	8.25	4.65	18	32 ⁵
Great Tit	18.5	18.3	2.4 ³	15	6.33	16	40
Dunlin	57.5	44	10.9	11-42	9.06	29-99	120
Herring Gull	1000	284	11.2	44	73.8	25	15

¹PE = productive energy.

²BMR = basal metabolism rate, calculated from appropriate equation for resting birds in Aschoff and Pohl (1970).

³Only the female incubates.

⁴Range 17-51%.

⁵Range 1.7-52% (34.4-14.5°C).

⁶Sources of data are, in order, Kendeigh (1963), El-Wailly (1966), Mertens (1967), Norton (1973), Drent (1970).

⁷El-Wailly calculated these values on the basis of the temperature gradient ($t_e - t_a$) between the eggs and room air, rather than between the eggs and nest air, which apparently was not measured.

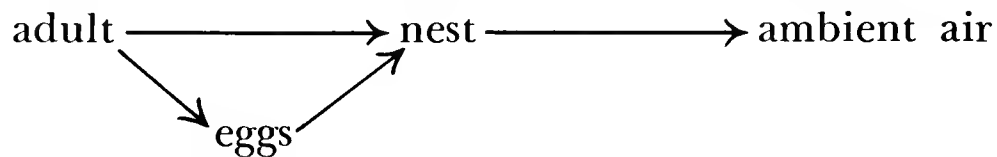
In the nest eggs lose heat to the air that surrounds the clutch, to the nest material, and to other eggs, if they are cooler. Thus, the eggs may partially insulate each other and reduce the cooling constant of each egg. Careful measurement of air temperatures surrounding the eggs in the nest largely obviates the need to measure cooling rates in the nest itself. Errors of estimation caused by the cooling constant may be quite small. For example, Kendeigh (1963) examined cooling rates of eggs in the nests of House Wrens during periods of parental inattentiveness and, allowing for changes in nest temperature during the period, found the cooling rate to be only about 7% less than that measured in the laboratory.

Loss of heat from the nest to the surrounding air may pose a greater problem, for adults must also maintain the temperature gradient between the nest and surrounding air, as well as between the eggs and the nest air. One could argue that nest air temperatures are maintained solely by the maintenance energy expenditure of the adult and energy applied directly to the eggs; that is, birds do not expend additional energy to elevate the temperature of the nest. This would seem the best position to take in view of the fact that most species have incubation patches for efficient heat transfer to the eggs. Warming of the eggs

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by direct application of heat is undoubtedly more efficient than reducing heat loss from the eggs by warming the nest.

If adults do not expend additional energy above maintenance requirements to warm the nest, the temperature of the air surrounding the eggs would represent an equilibrium between heat supplied to the eggs and heat dissipated from the nest, as follows:



The heat energy drawn from the nest by the ambient air is equal to the heat energy drawn from the adult by the eggs and the nest. Since the adult must maintain the temperature of the eggs and the nest, adult metabolism must vary with ambient air temperature. Nest temperature will be adjusted to the point that adult metabolism balances the loss of heat from the nest to the air. But since metabolic rate is adjusted in response to nest temperature, not ambient temperature, we do not need to measure the heat loss of the nest directly to estimate the energy requirement of incubation.

ENERGY REQUIREMENTS OF INCUBATION: CLUTCH WEIGHT METHOD

If we assume that the incubation patch permits heat transfer to the eggs as rapidly as heat transfer occurs within the body of the adult, and that the insulative properties of the nest are equivalent to those of the integument of the adult (if not better), we may estimate incubation energy requirements as being equivalent to maintaining the temperature of the same weight of body tissue. This approach has been used by West (1960) for the Tree Sparrow. West corrected for the fact that egg temperature was 7.5°C lower than body temperature by assuming a temperature coefficient of metabolism (Q_{10}) of 2.5. But since heat transfer to the egg is accomplished during early incubation only by conduction at the egg's surface (no circulatory system is present to distribute heat quickly), we may assume that the cost of maintaining eggs at the incubation temperature gradient above ambient temperature does not differ from the cost of maintaining body tissue at a similar gradient between adult core and ambient temperature.

Energy requirement for incubation may now be estimated from weights and temperatures of the adults and the eggs. Metabolism is calculated for any ambient temperature from the equation for conductance as a function of body weight

$$C(\text{cal/g} \cdot \text{hr} \cdot ^\circ\text{C}) = 4.0 W(\text{g})^{-0.508}$$

(Lasiewski, et al., 1967). Thus a 100 g passerine bird with a body temperature of 40°C requires 7.7 cal/g·hr to maintain its temperature

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at 20°C ($\Delta T = 20^\circ\text{C}$). If the clutch weight is 50 grams, 6.93 kcal/day (38% BMR) would be needed to maintain its temperature at 35°C.

Estimates of incubation energy requirements calculated in this manner (Table 18) are fairly close to estimates derived by Kendeigh's equation for open nesting species (Dunlin, Herring Gull) but are higher than those for cavity nesters (House Wren, Great Tit (*Parus major*)). My estimates for cavity nesters are based on 24 hours incubation per day, but females are probably attentive only about 75% of the day. This correction brings the clutch weight method estimates even closer to estimates based on Kendeigh's formula. El-Wailly's estimates of the incubation energy requirement of the Zebra Finch are too high because he used egg-room air temperature rather than egg-nest air temperature for the term $(t_e - t_a)$ in Kendeigh's equation. The estimates based on clutch weight are probably much more accurate.

Using the equations for conductance from Drent and Stonehouse (1971) and for BMR from Aschoff and Pohl (1970), we may estimate the incubation energy requirement as a percent of BMR by the equation

$$\text{Incubation requirement (\% BMR)} = 0.901 W(g)^{-0.19} (t_b - t_a) \times 100$$

for passerines, and

$$\text{Incubation requirement (\% BMR)} = 0.15 W(g)^{-0.20} (t_b - t_a) \times 100$$

for nonpasserines, where t_b and t_a are the body and ambient temperatures, respectively, and clutch weight is equal to body weight. These relationships are shown graphically in Figures 6 and 7. Incubation apparently places a proportionally smaller energetic strain on large birds than on small ones. For a given body size and temperature gradient, one can place a species on the graph to determine its incubation requirement for a clutch of eggs equal to its body weight. Unfortunately, we do not know how much energy can be made available for incubation, as a function of either adult body weight or ambient temperature. It is also difficult to determine whether average or maximum temperature gradients provide critical limits. If foraging rate determines available energy, temperature gradients averaged over several days should be more important; if metabolic energy mobilization or the capacity of tissues to generate heat determines heat production, short-term maximum gradients could be limiting. If a bird could generate heat for temperature regulation and incubation to the extent of 200% BMR, it could successfully incubate a clutch equal to its own weight at a temperature gradient at which the requirement for incubation was 150% BMR. The remaining 50% BMR would have to be added to the basal metabolism of the adult (100% BMR) to maintain its body temperature. Reducing the size of the clutch, or the rate of heat loss of the eggs and the adult, would permit incubation at greater temperature gradients.

TABLE 18
Estimates of Incubation Energy Requirements Calculated from Clutch Weight and Conductance.¹

Species	Weight (g)		Conductance (cal/g·hr·°C) ²	Temperature (°C)	Incubation requirement		
	Adult	Clutch			(kcal/pair·day)	% BMR	Kendeigh's formula (kcal/pair·day)
House Wren ³	10	8.2	0.989	17.1	3.48	86	2.20
				22.2	2.69	77	1.70
Zebra Finch ⁴	12.1	3.8	0.906	14.5	1.69	36 ⁶	4.78 ⁷
				20.9	1.17	25 ⁶	3.24 ⁷
				24.4	0.88	19 ⁶	2.47 ⁷
				29.1	0.49	11 ⁶	1.24 ⁷
				34.4	0.05	1	0.16 ⁷
Great Tit ⁵	18.5	18.3	0.744	ca. 20	4.90	77	2.4
Dunlin ⁵	57.5	44	0.439	ca. 5	13.91	153 ⁶	21.8
Herring Gull ⁵	1000	284	0.117	ca. 14	16.75	23 ⁶	22.4

¹ Assuming body temperature = 40°C and egg temperature = 35°C.
² Calculated by the formula, corrected for evaporative water loss, cal/g·hr·°C = 2.88 W(g)^{-0.464}.
³ Kendeigh (1963).
⁴ El-Wailly (1966).
⁵ Drent (1972).
⁶ Shared by both members of pair.
⁷ These values are incorrectly estimated and are too high (see text).

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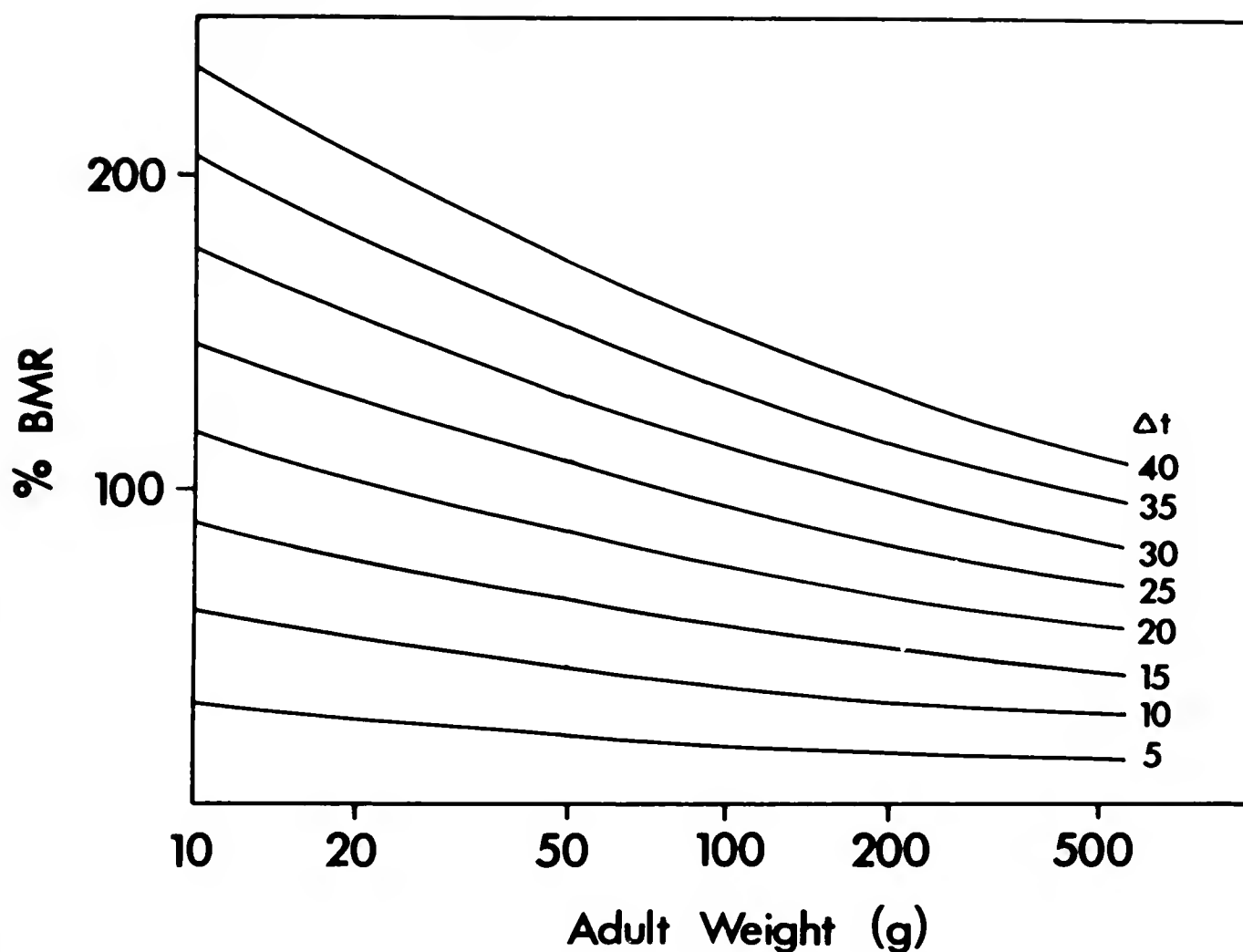


FIG. 6. Energy requirement (%BMR) for incubating a clutch of eggs equal to body weight (calculated by the clutch weight method) as a function of adult body size and gradient between body and ambient temperature. Values are calculated for passerine birds.

A general rule of thumb would be that an adult could incubate a clutch equal to its body weight at one-half the lethal temperature gradient, regardless of the productive energy available to it, so long as the bird was spelled frequently enough by its mate to obtain food. For example, the Zebra Finch apparently cannot incubate eggs successfully below 20.4°C (a gradient of about 19°C); its lower limit of temperature tolerance for existence is -1.3°C, a gradient of 41°C (El-Wailley, 1966). (A clutch of Zebra Finch eggs weighs only about one-third of the adult, however, suggesting either that the nest is poorly insulated or that the incubation behavior of Zebra Finches is not geared to cold temperatures.) Kendeigh (1963) suggested that the lower lethal temperature for the House Wren is about 0°C and that incubation cannot be accomplished successfully below 14°C. Heavy nest insulation permits the adult to allocate more of its available energy to incubation than the Zebra Finch and allows the wren to warm its eggs at temperature gradients greater than one-half the lethal gradient.

SOURCES OF HEAT FOR INCUBATION

The sources of heat energy for incubation are a controversial and unresolved problem. In a recent symposium on avian breeding biology,

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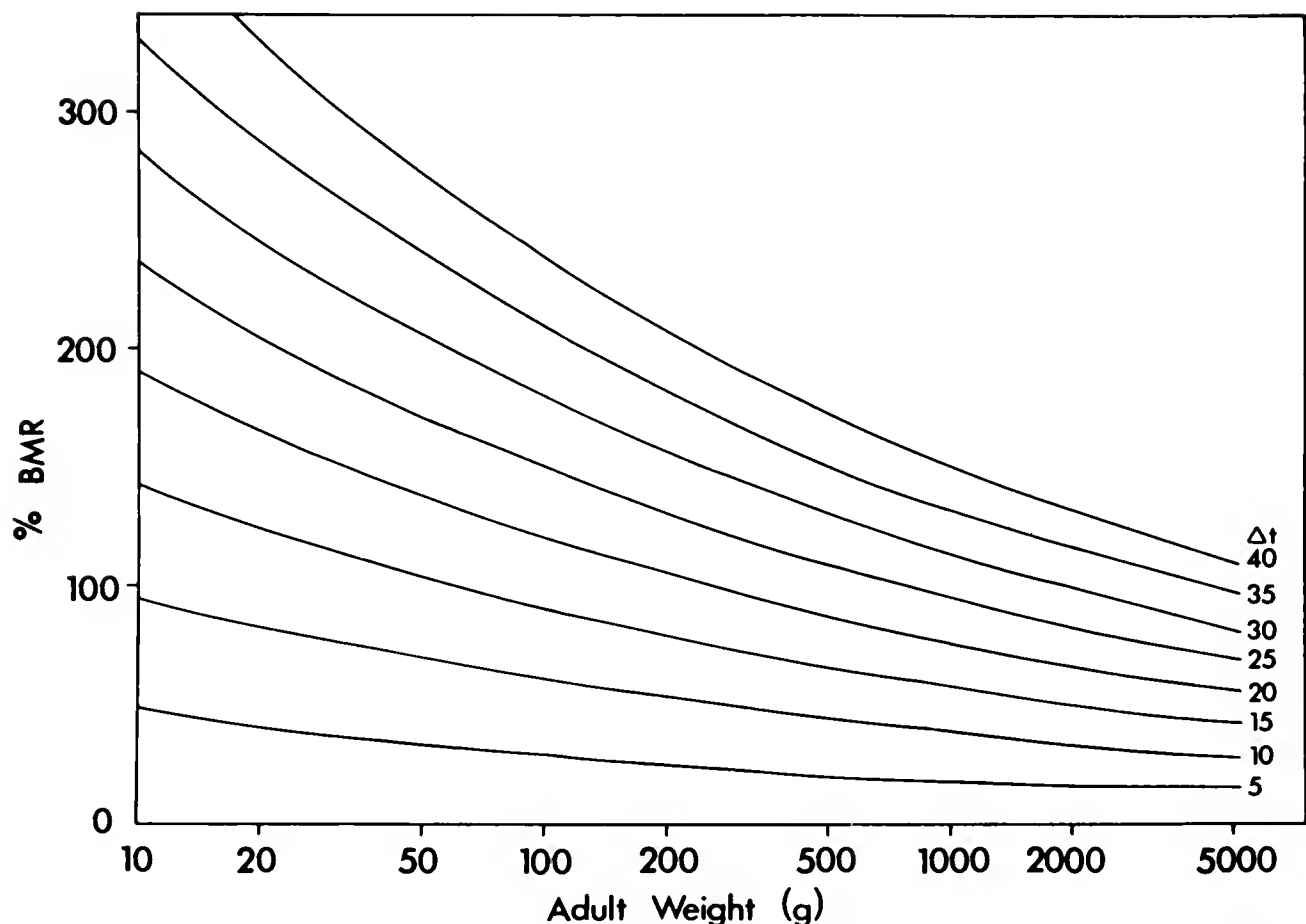


FIG. 7. Energy requirement (%BMR) for incubating a clutch of eggs equal to body weight (calculated by the clutch weight method) as a function of adult body size and gradient between body and ambient temperature. Values are calculated for nonpasserine birds.

King (1973:101) maintained “. . . it remains an open question as to whether or not a bird must significantly increase its energy expenditure for the specific purpose of incubating its eggs,” and further suggested that “. . . reproductive potential of a species is most sensitive to caloric shortage at the time of egg laying.” In the same volume, Kendeigh (p. 113) countered, “There is no question in my mind, contrary to the position taken by Professor King, that incubation carries an energy cost and that, if the energy is not available, reproduction will not take place.”

King and Kendeigh did not dispute the existence of an energy requirement for incubation, rather they differed over the source of energy to fill that need. The adult's capacity for generating heat is the most obvious source of heat, although King suggested that energy normally expended by the adult for maintenance and temperature regulation could be channeled to the eggs. But I favor Kendeigh's implicit argument that the energy requirement for incubation must be supplied largely by supplemental heat production, particularly in open-nesting species. Opening a heat gate through the brood patch to the eggs does not reduce the loss of heat through other surfaces of the body. The brood patch allows the rapid transfer of heat through a local area of skin without concomitantly increasing the general level of heat dissipation over the whole body. On the other hand, if incubation requires only 20-30% of the resting adult metabolism at a particu-

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lar temperature, as King has calculated, and if the incubation patch covers a similar percentage of the body surface, which may be nearly true for many species with large clutches, heat loss through the incubation patch at normal metabolic levels may be sufficient for incubation. However, King's percentage estimates may not be generally applicable because two of the species have relatively small clutches (Zebra Finches and Herring Gull) and one is a hole-nester (House Wren).

Certainly an enclosed nest, whether it is placed in a cavity or is a cup that is so deep it engulfs the incubating bird as well as the eggs, reduces heat dissipation from the body and allows the adult to allocate more energy to incubation. But the reduction of adult metabolism by increased insulation does not directly reduce the energy requirement for incubation or alter the fact that the adult must generate additional heat above the maintenance level required if it were merely roosting in the same nest.

The energy expended in incubation serves to raise the temperature of the eggs above ambient temperature into the range suitable for embryonic development. Heat for incubation can be supplemented in several ways. The most important of these sources for most species are the heat generated by the embryo itself and the radiational heat obtained directly from the sun. Kendeigh (1963) also lists atmospheric heat and a quantity referred to as "residual heat" as additional sources of energy. The atmosphere cannot contribute heat to eggs if they are warmer than ambient air. Kendeigh's atmospheric heat refers to a quantity of heat saved by the incubating adult when the air temperature is above the temperature threshold for development (17.2°C in the case of the House Wren; see Kendeigh, 1963). Although the temperature threshold may have important developmental implications, it has no place in the heat budget of incubation. Kendeigh's residual heat, defined as the heat retained in the nest owing to its insulation, is similarly not a source of heat. It is merely a measure of the saving of energy compared to a situation in which eggs were incubated without a nest, or any form of insulation.

Absorption of radiant energy by the nest clearly replaces part of the heat lost from the nest to ambient air and reduces the heat that the adult must provide. Kendeigh (1963) demonstrated the influence of direct sunlight on nest temperatures in the House Wren. But since the nests of so many birds are built in the shade, and since all birds must incubate during the night, it seems doubtful that possibilities of obtaining solar heat have played a major role in the evolution of incubation behavior. On the contrary, the role of insulation in energy conservation may be overshadowed by problems of heat dissipation for most species.

Heat generated by the developing embryo is potentially a more important and general source of heat than insulation. Since this source

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becomes well developed only toward the end of the incubation period, it probably has not been a major factor in the evolution of incubation patterns.

Drent's (1970) study on the Herring Gull is the most complete analysis of the contribution of embryonic heat to incubation temperature, although heat production of the egg has been measured for the House Wren (Kendeigh, 1940), the domestic fowl (Romijn and Lokhorst, 1956, 1960), and a duck (Kashkin, 1961). Figure 8 shows Drent's

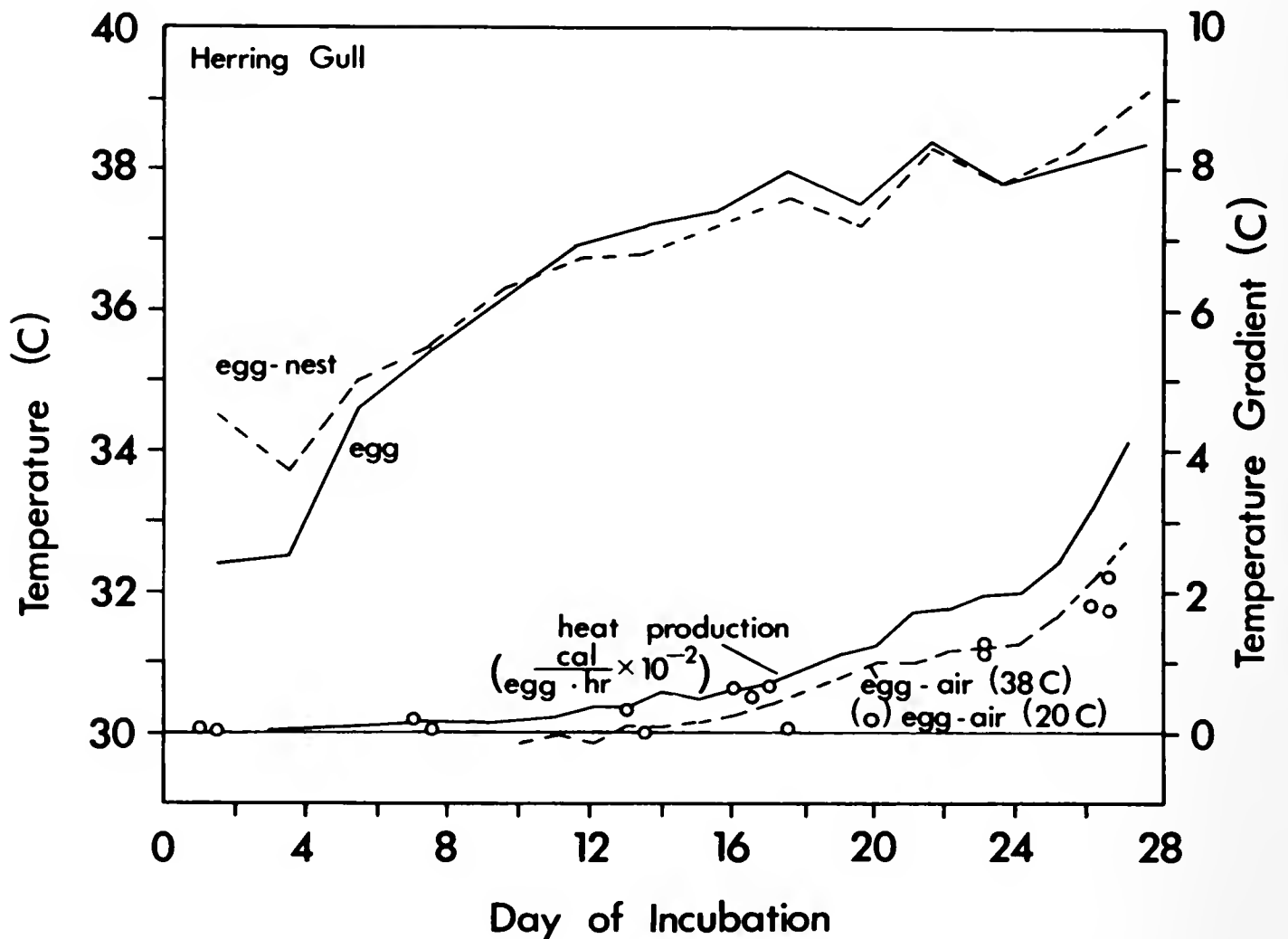


FIG. 8. Temperature of eggs in the nest, egg-nest air temperature differential, egg-air temperature gradients in chambers at 38°C and 20°C, and heat production of the embryonic Herring Gull as a function of day of incubation (after last egg is laid). Scale for egg temperature is at left. Scale for temperature differentials and heat production is at right. From Drent, 1970.

data for embryonic heat production at 37°C (incubator temperature), temperature excess maintained by the egg at ambient temperatures of 20 and 38°C, and the temperature of eggs in the nest. The temperature of eggs in the nest increases by about 4°C during incubation; thus the heat which must be supplied to warm the egg also increases. Drent suggested, on the basis of calculations using Kendeigh's formula, that the energy requirement of incubation about doubles, increasing from 0.7 to 1.5 kcals/hr during the incubation period. This increase must be absorbed primarily by adult metabolism because embryonic heat production does not increase substantially until later in the incubation period.

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As the Herring Gull embryo approaches full term its rate of heat production contributes a substantial proportion of the incubation requirement (Fig. 9). On the last day of incubation, each egg requires

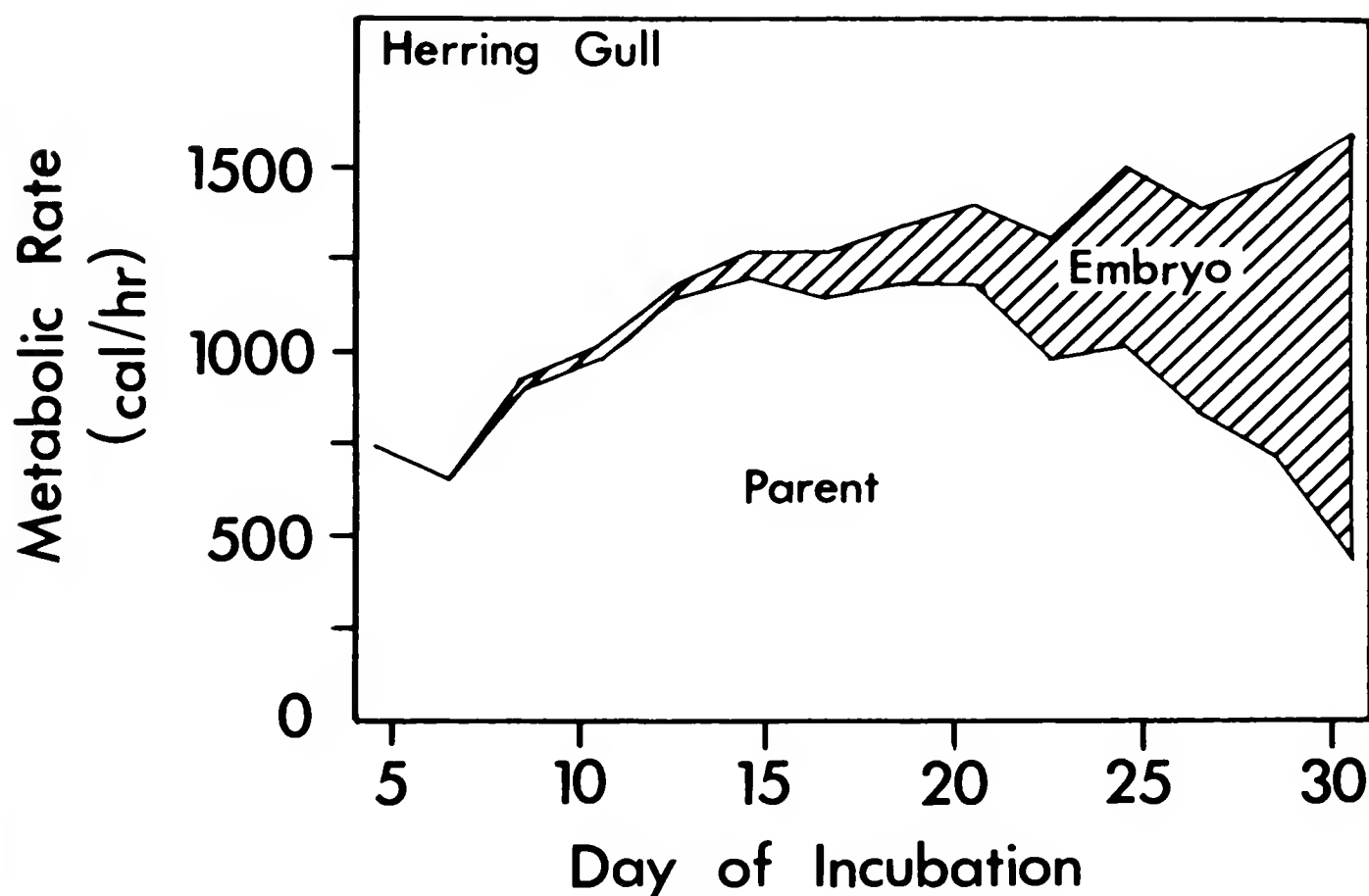


FIG. 9. Total energy requirement of incubation (calculated by Kendeigh's formula) and heat production of Herring Gull embryos during the incubation period. From Drent, 1970.

545 cal/hr of which the embryo provides 411 cal/hr, or 75% of the total. However, some discrepancies occur in calculations based on Drent's data. For example, the full term egg is observed to maintain a temperature gradient of 2.69°C at 38°C . But one would expect, from data on rate of heat loss and embryonic heat production, a gradient of 5.62°C at 38°C . This value is calculated from the relationship (derived from Kendeigh's equation)

$$\frac{1}{(t_e - t_a)} = \frac{W \cdot h \cdot b}{\text{heat production}}$$

or

$$\frac{1}{(t_e - t_a)} = \frac{83.8 \times 0.8 \times 1.09}{411.2} = \frac{1}{5.62}$$

where W = weight of the egg, h = specific heat of the egg and b = the cooling constant. The cooling constant is the most suspicious value but I cannot find the source of the discrepancy, and Drent's methods appear to be impeccable. Even if we replace the cooling constant by $1.73^{\circ}\text{C}/^{\circ}\text{C}\cdot\text{hr}$, a value determined empirically in a respiration chamber with circulating air, we expect the egg-air gradient to be 3.54°C which is still greater than the observed 2.69°C .

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Kendeigh (1963) discounted metabolism of the embryo as an important source of heat for incubation, but his data for oxygen consumption of House Wren embryos (Kendeigh, 1940) indicate that the egg contributes 26, 48, and 75% of the heat required for its own incubation on days 7, 10 and 12, respectively, of the incubation period (14 days). Although embryonic heat production cannot reduce any limitations posed by incubation soon after the clutch is completed, it can free the parent to channel its time and energy in other directions during the latter part of the incubation period.

DIRECT MEASURES OF INCUBATION ENERGY EXPENDITURES

In view of the difficulties with assumptions needed to calculate the energy requirement of incubation indirectly, direct measurement of metabolic rates of incubating adults seem necessary to fully resolve the cost of incubation. Several methods are possible, including measurement of food consumption of penned or caged birds during incubation, and measurement of gas exchange by means of doubly-labelled water (D_2O^{18}) or gas analyzers. Long term measures of metabolism (food consumption D_2O^{18}) include all the activity of the bird during the incubation period, not just metabolism while the bird is on the eggs. Direct measurement of gas exchange can only be applied to species that will incubate within a metabolism chamber or a nest box modified for gas analysis.

By measuring food consumption, Riddle and Braucher (1934) and Brisbin (1969) found no increase in metabolism during the incubation period of Common Pigeons (*Columbia livia*) and Ringed Doves (*Streptopelia risoria*), even though individuals of both species are about 8% heavier during the incubation period than during non-reproductive periods. However, the clutch weight of the Ringed Dove (2 eggs) is only 6.6% of adult weight, and one might expect that the incubation energy requirement could be fulfilled entirely by normal heat loss from the adult; doves do not even form an incubation patch (Jones, 1971).

El-Wailly (1966) found that Zebra Finches increase their food consumption during incubation by 11.7, 12.8, 13.6 and 0% over existence energy during control periods at temperatures of 20.9, 24.4 and 29.1, and 34.4°C, respectively. The absolute increases in metabolic rate of 3.0, 2.1, 1.5 and 0 kcal/pair per day, respectively, are greater than my predictions of 1.17, 0.88, 0.49, and 0.05 (see Table 18), but nonetheless constitute only a minor increment of energy expenditure.

Several attempts have been made to measure the oxygen consumption of birds sitting on eggs. The simplest procedure is to work with hole nesting birds, where a nest box can be converted into a metabolism chamber. Drent (1973) quoted unpublished data of Mertens (1967) which was obtained in this manner for the Great Tit. Oxygen consumption was measured continuously for females incubating at night by drawing air through the nest box and into an oxygen analyzer. Outside (ambient) air temperature varied from 16-23°C, and the

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temperature in the nest box remained between 27-34°C, which is within the thermoneutral zone of the adult. Metabolism decreased linearly with increasing ambient temperature as one would expect, from about 255 cal/hr at 15°C to 150 cal/hr at 24°C. But the expected metabolic rate of a 19 g bird within its thermoneutral zone is about 269 cal/hr (Aschoff and Pohl, 1970) and it seems unlikely that an incubating female in a nest box at 15°C could have a metabolic rate substantially below BMR.

I have experienced a similar problem in attempting to measure the metabolism of incubating Starlings. Air was drawn at about 600 cc/min through a large plastic nest box, with a 1¾ inch entrance hole located about 10 inches above the incubating bird. Temperatures in the air of the box above the bird were approximately the same as the ambient air; the temperature of the nest material under the eggs was maintained at about half the gradient between the adult and the ambient air (e.g., 22°C at 5°C ambient). Oxygen consumption decreased with increasing ambient temperature from about 160 cc/hr at 5°C to 40 cc/hr at 20°C; again, these values seem too low compared to an estimated BMR of 158 cc O₂/hr (Aschoff and Pohl, 1970). Apparently nest air diffused through the opening more rapidly than it was drawn through the box.

Norton (1973) devised a plastic dome that could be dropped over an incubating female Baird's Sandpiper. The dome was hooked up both to an open flow and a closed flow system, and a series of reasonable measurements of oxygen consumption were obtained (Table 19). The resting metabolic rate of an adult at temperatures in the chamber should have been about 280 cc O₂/bird hr, and Norton used Kendeigh's formula to estimate the energy requirement for incubation at 150 cc

TABLE 19

Oxygen Consumption (ccO₂/bird · hr) of an Adult Baird's Sandpiper Incubating a Clutch of 4 Eggs (after Norton, 1973).¹

Day of incubation	Open flow system		Closed system	
	Adult plus		Adult plus	
	4 live eggs	4 dead eggs	4 dead eggs	4 live eggs
19	308	252		
20		277	290	
21	419		310	96

¹Temperature inside chamber 6-10°C; normal ambient temperature 0-5°C.

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O₂/hr. Calculations based on the clutch weight method results in a somewhat lower prediction. Metabolic rates obtained by the open and closed systems compared favorably (277 vs 290, and 419 vs 310 cc O₂/hr). Metabolic rates obtained just after adults returned to incubate cooled eggs were higher (480-650 cc O₂/hr) although this increment could have resulted from the restoration of an oxygen debt after activity, rather than increased heat production to warm the eggs.

Norton felt that observed rates of oxygen consumption should have been higher ($280 + 150 = 430$ cc O₂/hr), but commented that "In view of the measured rates which are lower than expected, one either has to question whether incubation cost is additive to RMR (resting metabolic rate), or to regard the experimental results with suspicion." This approach promises to be fruitful, however, and should be pursued vigorously.

INCUBATION BEHAVIOR OF THE ADULTS

The energy requirements and thermal characteristics of incubation exert a strong influence on adult incubation behavior. The relation between ambient temperature and percent of time the eggs are incubated is well known (Kendeigh, 1952; von Haartman, 1956). Different species vary the length of attentive periods, or inattentive periods, or both. The degree to which incubation rhythms are dictated by environmental conditions was elegantly demonstrated by Johnson (1971) in experiments on the comparative incubation behavior of the Starling and Myna (*Acridotheres cristatellus*) at Vancouver (summarized by Drent, 1972). Both species are introduced, the Starling from areas in Europe with a temperature regime similar to that of Vancouver (9°C average during the incubation period), and the Myna from Hong Kong, where temperatures average 25°C. Mynas do not adapt their incubation rhythm (60% attentiveness during daylight hours) to Vancouver's climate and hatching success in the study was only 58%. Hatching success of the Starling (79% attentiveness) was 82%. Incubation failure in the Myna was not linked to any inherent quality of the eggs because Starlings could successfully incubate Myna clutches easily, but not vice versa. When Johnson artificially heated Myna nest boxes to 28°C, however, hatching success rose to 92%.

The proportion of time that must be spent incubating depends largely on how rapidly eggs cool if left unattended and, therefore, is a function of ambient temperature and nest insulation. If the eggs must be covered for such a large fraction of the day that a single incubating bird could not gather its required food in the period off the nest, both parents must incubate and the eggs are frequently covered continuously. It is not surprising that in hole nesters (such as the House Wren and Great Tit) and tropical species the burden of incubation is frequently assumed by only one member of the pair.

Even if it were possible for adults to remain off the nest for a considerable period, the cooling characteristics of their eggs may greatly

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limit the permissible length of inattentive spells. Thus a bird may be forced to divide its off time into small intervals rather than a single long interval (Drent, 1973). Eggs of Herring Gulls warm more slowly after a parent returns to the nest than they cool when the adult leaves. Kendeigh (1963) also found that eggs of House Wrens in the nest cool more (1.3 times) rapidly than they are warmed. Heat transfer from the brood patch to the egg is undoubtedly more efficient than from the egg to the open air, but eggs lose heat over their entire surface and gain heat only through that portion of surface area (18%-25%) in contact with the brood patch. The egg also loses heat to the surrounding nest air while it is being warmed by the parent. Drent (1973) suggested that birds might compensate for relatively slow warming rates by keeping absences to a minimum, usually less than one minute in the Herring Gull. But since other species leave their clutches unattended for periods of from 10 minutes to an hour, it would seem that ambient temperature, and whether one or both adults incubate, are more important factors in determining the length of absences than the rate of egg warming.

In most species of arctic sandpipers, both parents incubate and eggs are covered almost continuously. In the Pectoral Sandpiper (*Calidris melanotos*), only the female incubates, and she is attentive at the nest an average of 85% of the day (Norton, 1972). During the cooler hours of the "night," incubation is almost continuous; during the lighter and warmer hours of the day 5-10 minute absences spaced between 20-40 minute attentive periods allow the females to obtain enough food to maintain their body weight under normal weather conditions. Several single-sex incubators in the tropics also maintain 85% attentiveness over 24 hours, but in the Arctic such incubation schedules must place adults close to their foraging limits and place eggs close to their temperature limits. Both Norton (1972) and Weeden (1966), who studied Tree Sparrows, have noted a general breakdown of incubation performance during adverse weather.

In many species with either incubation by one sex or very prolonged incubation spells, birds subsist on stored fat (penguins) or are fed by their mates. Males of many birds of prey forage both for themselves and their mates during the incubation period, but in times of food shortage, females may be forced to abandon incubation and forage themselves (Cavé, 1968; Southern, 1970). Nelson (1969) has suggested that in the Red-footed Booby (*Sula sula*) on the Galapagos Islands, where both sexes incubate but spells are long (2-3 days), marginal feeding conditions were responsible for the high rate of desertion during the incubation period. Adults that finally abandoned nests, exposing the eggs to predators and the sun, had been at the nest for two to three times the normal incubation spell. Presumably their mates had not returned owing to poor foraging conditions at sea. Hornbills (Bucerotidae) show the extreme separation of incubation and foraging roles within the pair. The female is actually sealed into

the nest, which is placed in a cavity, where she is fed through a small hole by her mate.

One member of a pair, usually the male, feeding its mate at the nest has been recorded in many groups: These include, among others, the Falconiformes, Coraciiformes, Corvidae, Paridae, Sittidae, some Turridae (not including *Turdus*), Laniidae, some Parulidae, and many Fringillidae (Lack, 1940). The habit has not been recorded in species that have been studied in the Procellariiformes, Pelicaniformes (except Tropicbirds), Ciconiiformes, Galliformes, Charadriiformes, Apodiformes, Picidae, and Passeriformes (Tyrannidae, Hirundinidae, Troglodytidae, Mimidae, Sturnidae, Vireonidae, Ploceidae, and Icteridae). The distribution of incubation feeding has no obvious taxonomic or ecological pattern. In fact, the frequency of feeding of mates in most groups is probably so low that the behavior probably has no important energetic purpose and may be a display serving to maintain the pair-bond.

Among species in which both parents incubate, the length of the spell may be determined partly by foraging behavior. For example, Drent (1965) has pointed out that seabirds which feed at considerable distances have long incubation spells. Pigeon Guillemots (*Cepphus columba*) feed close to shore and incubation spells are usually less than two hours. On the other hand, Common Puffins (*Fratercula arctica*) may feed as far as 80 miles from their nesting colonies (Pearson, 1968) and have incubation shifts of 23 to 70 hours, with a mean of 33 hours (Myrberget, 1962). Species that return to their colonies only at night, such as Leach's Petrel (Wilbur, 1969), break their incubation shifts into multiples of 24 hours. Gross (1935) stated that 96 hours (4 days) is the normal spell in Leach's Petrel, a species that feeds more than 100 miles from the nesting colony at Kent Island, New Brunswick.

When air temperatures approach the natural incubation temperature of the egg, parents may have to shade the eggs, without actually contacting them, if overheating in the sun is to be prevented (e.g., Howell and Bartholomew, 1962). If the air temperature rises above the normal incubation temperature, adults may have to sit on the eggs to remove heat (Franks, 1967). In this case the egg temperature cannot be maintained below the temperature of the brood patch and, in fact, must be somewhat higher because of the inefficiency of heat transfer from the egg to the skin. For example, Russell (1969) found that at air temperatures of 42-43°C brood patch temperatures of White-winged Doves (*Zenaida asiatica*) were 38-39°C and eggs were maintained between 39.0 and 39.3°C. Adult doves are able to maintain body temperatures below air temperature by evaporative cooling, particularly with gular flutter (Bartholomew, et al., 1968), but it seems unlikely that the body core would be maintained as low as 38-39°C. This raises the possibility that the ventral apteria of doves may be cooled directly by evaporative water loss from the skin.

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ENERGETICS OF GROWTH

Patterns of energy utilization from hatching to independence of the young have two components: the allocation of time and energy by the parents to food gathering and direct care of the young, and the use of energy by the young themselves. These components are intimately related through strategies of development and parental care. In this section we shall concentrate primarily on the use of energy by the young and how this is related to the pattern of development.

Developmental patterns of birds range from the altricial mode exemplified by most passerines to the precocial mode exemplified by galliformes. Virtually all intermediate forms occur. The pattern of development has traditionally been defined by the condition of the young bird at hatching (Nice, 1962). Precocial species hatch with a down covering, their eyes are open, and they typically can forage for themselves with a minimum of adult attendance. On the other hand, altricial species hatch naked and blind, and the young are dependent upon their parents for food and body heat. Precocial species generally develop more slowly than altricial species of similar size, although the pattern of development after hatching appears to be almost as important as the initial condition at hatching in determining the rate of growth (Ricklefs, 1973a). In general, species that exhibit early development of locomotor ability grow relatively slowly, as if embryonic, or growth processes compete with mature maintenance functions for the allocation of energy and tissues. An optimum balance between growth and maintenance functions must depend on how these patterns affect energy utilization by the young and the care that must be provided by the adults. We must ask, for example, why young gulls and terns, which are fed by their parent, have not adopted a more altricial mode of development. Why are altricial species not more self-sufficient, particularly why do they not maintain their own body temperatures? The following sections on the development of temperature regulation and the energetics of growth will provide much of the empirical data needed to discuss patterns of development and parental care.

Early self-sufficiency in maintaining body temperature requires the expenditure of energy by the young, but also frees adults to forage longer. The transition to full temperature regulation should ideally occur when the net result of these factors is to improve the overall energy balance of the family unit. We must also recognize, however, that birds generate heat by shivering and must have well-developed muscular and nervous systems to regulate their own temperatures. The development of temperature homeostasis must, therefore, parallel other aspects of development, particularly locomotor ability.

DEVELOPMENT OF TEMPERATURE REGULATION: PRECOICIAL SPECIES

The ability of newly hatched young of precocial species to regulate their body temperatures varies considerably, being greatest in the

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ducks, intermediate in galliform species, and least in shorebirds, particularly gulls and terns.

Neither chickens nor Herring Gulls show thermostatic responses to cooling as embryos (Romijn and Lokhorst, 1955; Drent, 1970). Although galliforms and charadriiforms both exhibit well-developed homeothermic responses immediately after hatching, their capacity for maintaining gradients between body and air temperature is quite limited and their propensity to regulate body temperature may occasionally lapse even at relatively high ambient temperatures. One-day old Herring Gull chicks can maintain a maximum temperature gradient of 12°C under laboratory conditions (Drent, 1970); newly hatched terns and Black-headed Gulls (*Larus ridibundus*) have a similar capacity (LeCroy and Collins, 1972; Keskpaik and Davidov, 1966). Young California Gulls cannot fully regulate body temperature at an ambient temperature of 10°C until about a week after hatching (Behle and Goates, 1957) but the more rapidly growing Common (*Sterna hirundo*) and Roseate Terns (*S. dougallii*) can maintain high body temperatures at ambient temperatures as low as 17°C by the fourth day after hatching (LeCroy and Collins, 1972).

Homeothermic capacity also increases gradually in galliforms (Bernstein, 1973). Coturnix Quail chicks are able to maintain high body temperatures at ambient temperatures as low as 20°C after a week and at ambient temperatures between 0 and 10°C after two weeks (Fig. 10, unpublished data). Pheasant chicks, when exposed to temperatures of 20°C for 30 minutes, cannot maintain their body temperatures above 35°C until they are 10 days old (temperatures are normally $39-40^{\circ}\text{C}$ in brooders). Regulation is very strong (maintaining 38°C at 5°C ambient) by the time the young pheasant are 3 weeks old (usually over 100 grams body weight; Ryser and Morrison, 1954). Rock Ptarmigan (*Lagopus mutus*) chicks are brooded extensively during the first week after hatching and are able to forage for only about an hour and a half each day until homeothermic capacities are well enough developed that the young are thermally independent of their parents (Theberge and West, 1973).

Temperature regulation is relatively well-developed in newly hatched ducklings, although there is considerable variation between species (Koskimies and Lahti, 1964; Cain, 1972). Newly hatched ducklings of most species can maintain normal body temperatures when exposed to 10 or 20°C temperatures for 20 minutes, whereas the body temperatures of newly hatched gallinaceous species dropped $1-3^{\circ}\text{C}$ at 20°C and $4-8^{\circ}\text{C}$ at 10°C (Koskimies and Lahti, 1964). Gallinaceous chicks are also brooded much more than ducklings. Thermogenic capacities are present, although weakly, in advanced duck embryos (Fig. 11). Initial signs of homeothermy appear as early as 20 days in the domestic duck (incubation period 27 days).

Sea ducks possess full thermoregulatory capacity at an earlier age than pond ducks. For example, when newly hatched Mallard duck-

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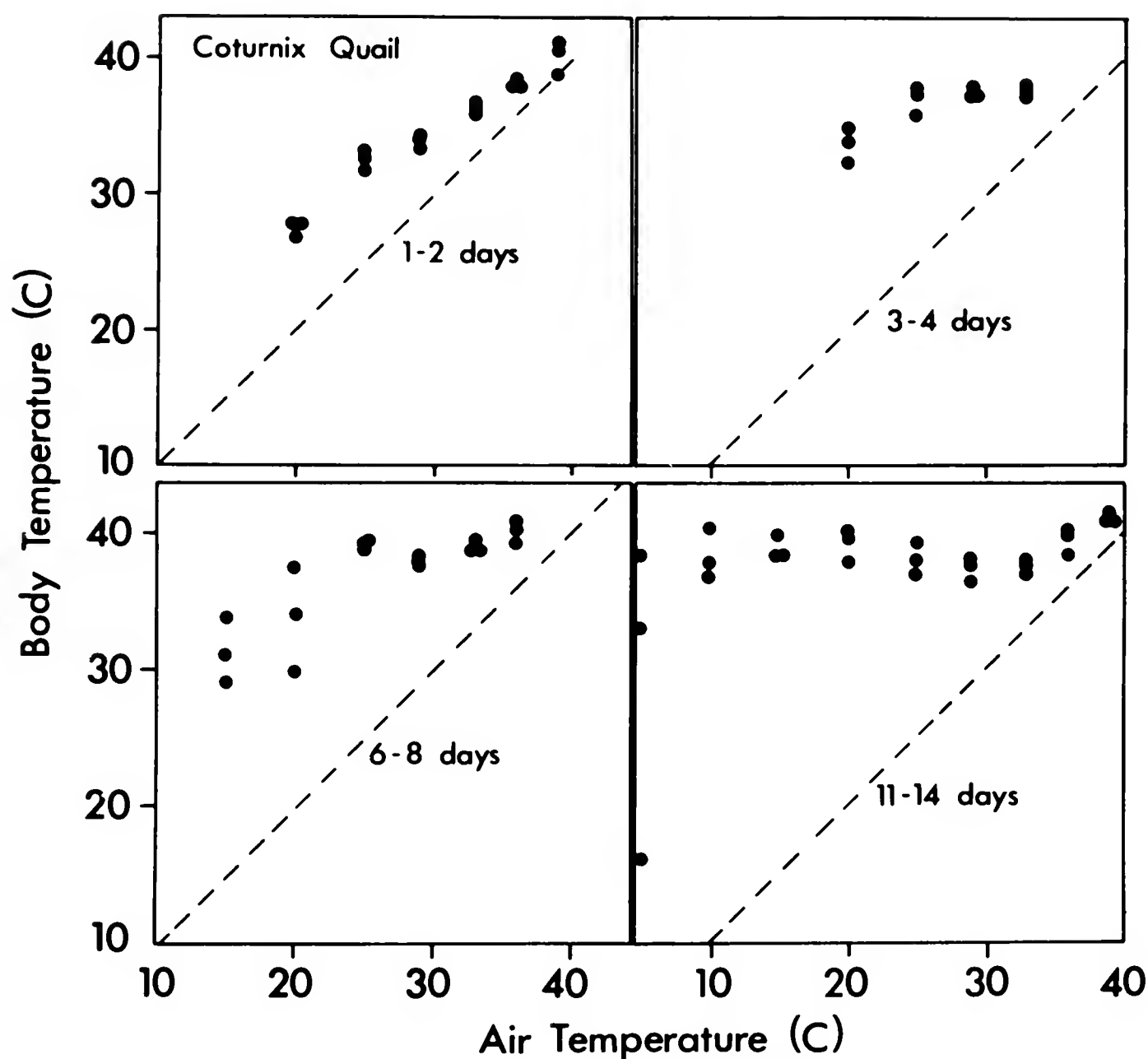


FIG. 10. Body temperature of Coturnix Quail chicks after exposure to a range of ambient temperatures for a period of one hour from hatching to two weeks of age (Ricklefs, unpubl.). The dashed diagonal lines represent body temperatures equal to ambient temperatures.

lings were exposed to an air temperature of -2°C , body temperature began to drop almost immediately. Five and 14 hours were required for such a drop in two White-winged Scoter (*Melanitta deglandi*) ducklings, and an American Merganser (*Mergus merganser*) duckling showed no sign of temperature drop after 15 hours. Koskimies and Lahti (1964) summarized metabolic characteristics of newly hatched young for 10 species of ducks (Table 20). The index of insulation (critical gradient/BMR) is lowest in species of *Anas* and highest in the Eider (*Somateria mollissima*), and corresponds to the relative ability of these species to resist cooling. Koskimies and Lahti also drew parallels between the thermoregulatory ability of ducklings and their geographical distributions. The capacity of ducklings to regulate body temperature is greatly enhanced by the distribution of the thickest downy plumage on the ventral surface and the prevention of heat loss through the feet by countercurrent circulation of blood in the legs (Irving and Krog, 1955).

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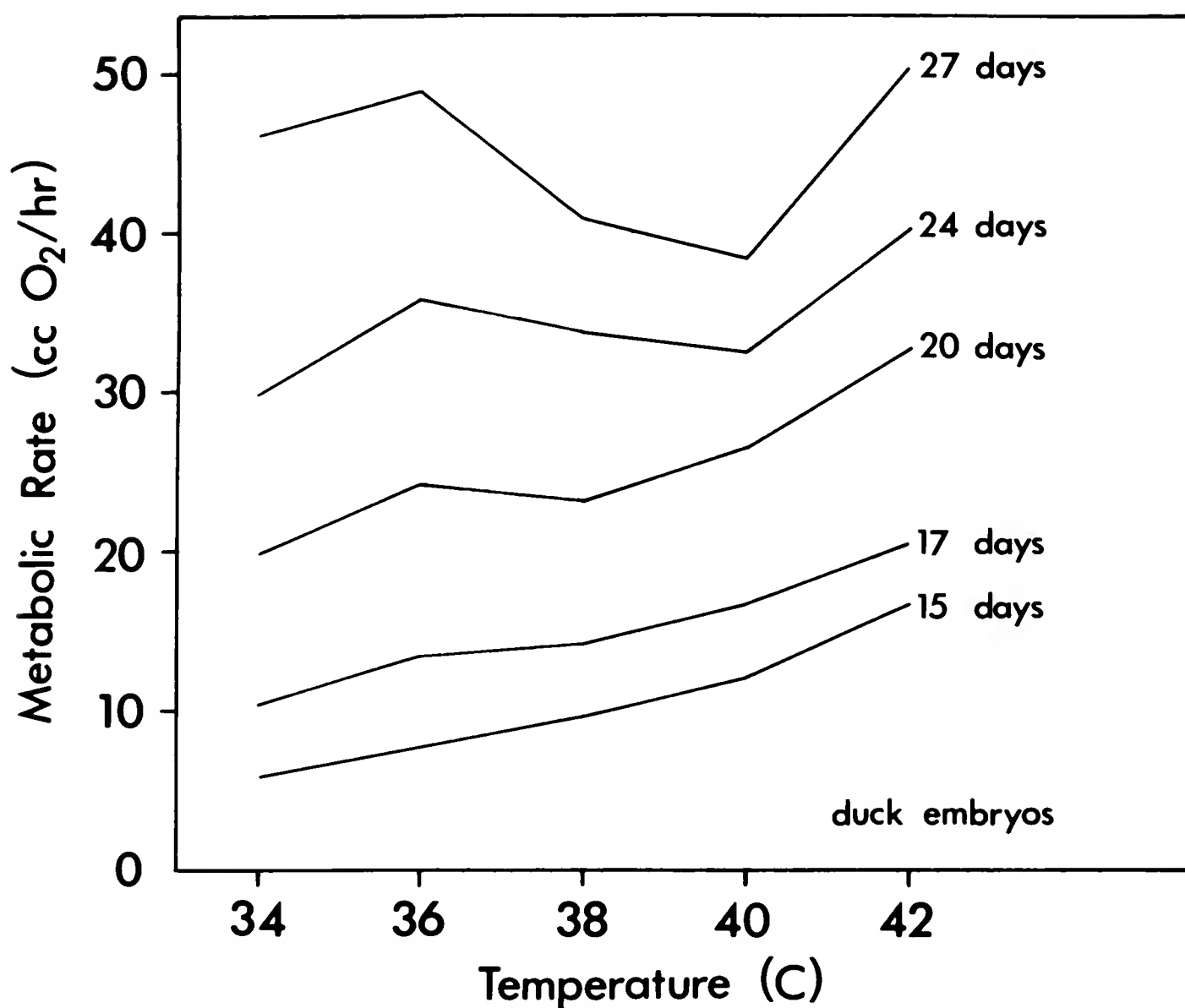


FIG. 11. Metabolic rates of domestic duck embryos over a range of incubation temperatures as a function of age (after Kashkin, 1961). A weak homeothermic response is observed as early as 20 days.

The ontogeny of thermoregulatory capacity can be measured by changes in the thermal conductance of birds as they grow (Fig. 12). Conductance is a measure of the rate of heat loss from the body, usually expressed in terms of $\text{cal/g} \cdot ^\circ\text{C} \cdot \text{hr}$, and it may be calculated either from rates of cooling or from metabolic rates of birds maintaining constant body temperature. In Figure 12, conductances of the young of several species are compared to regressions for live adults based on metabolism and for dead, defeathered adults based on cooling rate. As we shall see below, young of altricial species tend to have high conductances until they are fairly well grown. The conductance of newly hatched precocial young species varies in relation to their capacity to regulate body temperature. Young Baird's Sandpipers and Herring Gulls lose heat about 2.5 times as fast as adult birds of similar body weight. The insulative capacity of sandpiper chicks increases with growth, until it is comparable to that of adults of comparable size after about one week. Even so, the thermoregulatory capacity of sandpiper chicks is closely tied to activity. Norton (1973) found that young of several species of *Calidris* sandpipers at Barrow, Alaska, maintained body temperatures of $34\text{--}39^\circ\text{C}$ (average 37.2°C) when brooded, $30\text{--}38^\circ\text{C}$

TABLE 20
Thermal and Metabolic Characteristics of Newly Hatched Ducklings (after Koskimies and Lahti, 1964).

Species	Body weight (g)	BMR (cal/g·hr)	Critical gradient ¹ (°C)	Index of insulation ² (°C·hr·g/cal)	Conductance (cal/g·hr·°C)
<i>Anas platyrhynchos</i>	28.8	5.8	5.3	0.91	1.10
<i>Anas crecca</i>	16.8	8.7	6.1	0.70	1.43
<i>Aythya fuligula</i>	34.1	6.7	7.9	1.18	0.85
<i>Mergus serrator</i>	44.2	7.1	9.6	1.35	0.74
<i>Mergus merganser</i>	46.2	6.3	8.4	1.33	0.75
<i>Aythya ferina</i>	40.1	6.9	8.1	1.17	0.85
<i>Anas penelope</i>	26.4	8.8	8.9	1.01	0.99
<i>Somateria mollissima</i>	61.4	6.1	11.8	1.94	0.52
<i>Bucephala clangula</i>	32.4	8.6	9.6	1.12	0.89
<i>Melanitta fusca</i>	54.7	7.4	10.2	1.38	0.72

¹ Lower critical temperature minus body temperature (range of body temperatures, 37.2–39.3°C).
² Critical gradient/BMR.

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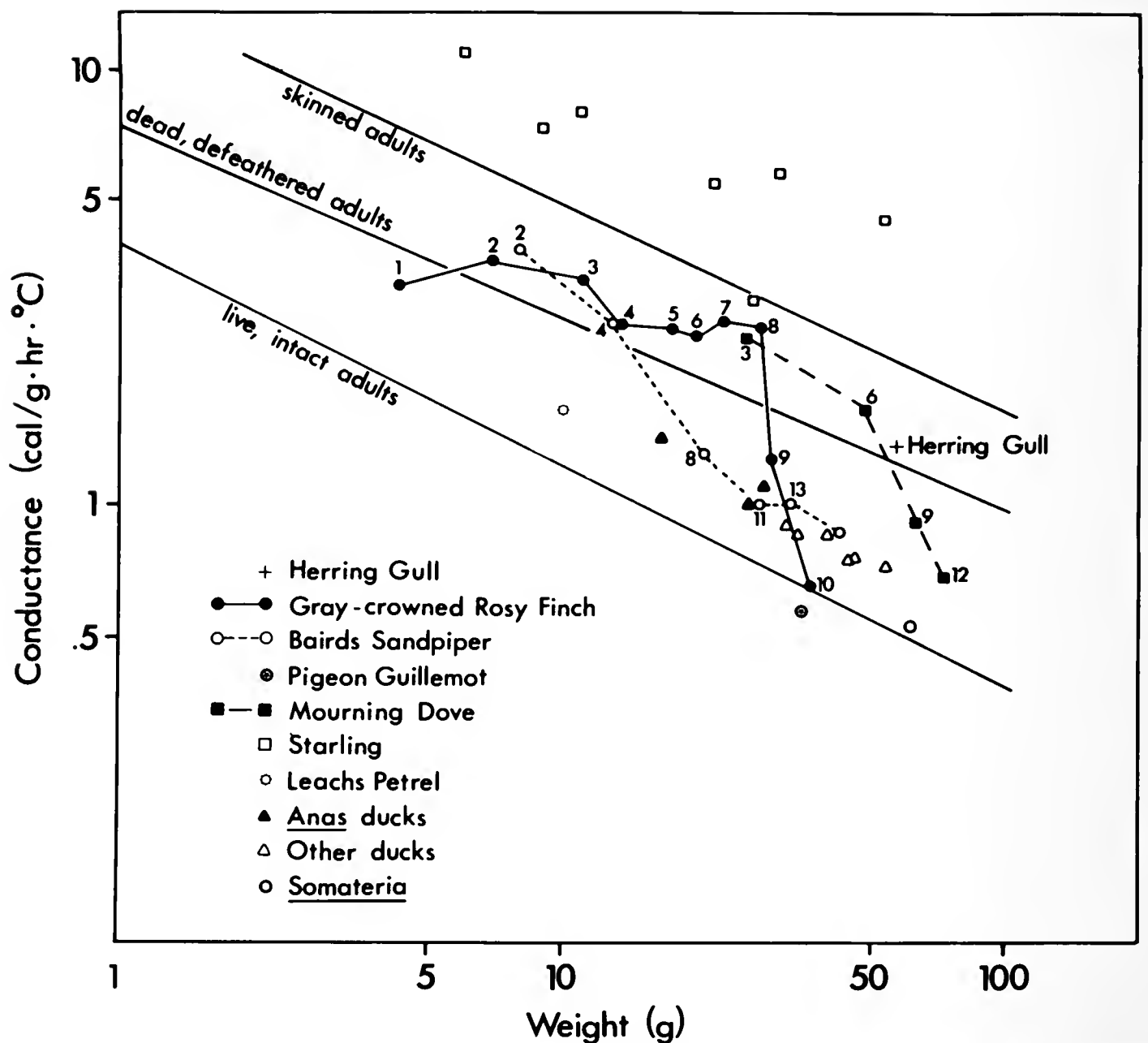


FIG. 12. Conductance of young of several species of birds as a function of body weight. Regressions are also shown for live adults based on data in Lasiewski, et al. (1967) and for dead, defeathered adults based on data in Herreid and Kessel (1967). Sources of data: Baird's Sandpiper (Norton, 1973); Mourning Dove (Breitenbach and Baskett, 1967); Herring Gull (Drent, 1970); Pigeon Guillemot (Drent, 1965); ducks (Koskimies and Lahti, 1964); Gray-crowned Rosy Finch (Yarbrough, 1970); Starlings and Leach's Petrels (Ricklefs, unpubl.).

(av. 34.3°C) when actively feeding, but only 23-31°C (av. 28.6°C) if they had been immobilized by parental warning upon the observer's approach and were located by their distress calls.

Leach's Petrels and Pigeon Guillemots (*Cepphus columba*) can maintain high body temperatures just after hatching and neonates of both species have low conductances—comparable to those of adult birds of similar size. Two-day old petrel chicks can maintain their body temperatures above 38°C when exposed to 20°C air, although they do not always do so (Ricklefs, White, and Cullen, unpublished). The young are brooded for the first few days after hatching. The development of thermoregulation is similar in the Pigeon Guillemot (Drent, 1965; Koelink, 1972) and other species of alcids and gulls (Rolnik, 1948; Kaftanowski, 1951) although its specific timing varies.

Conductance of duck hatchlings may be calculated from the data of

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Koskimies and Lahti (1964; Table 20) as the inverse of their index of insulation. The conductances of Mallard (*Anas platyrhynchos*) and European Teal (*Anas crecca*) ducklings are relatively high; only the Eider is appreciably lower than the other species of diving ducks and the European Widgeon (*Anas penelope*). Duck hatchlings, as a group, have low conductances at hatching. Koskimies and Lahti (1964) point out that the greater thermal independence of young diving ducks has led to the evolution of loose family ties and formation of combined broods of up to 50 young. Furthermore, young diving ducks often leave their parents before they are able to fly—a phenomenon never observed in surface feeding ducks.

Conductance is difficult to measure for gallinaceous species because the young only partially regulate body temperature at hatching. That is, the young exhibit a well-developed thermogenic response down to a fairly low temperature, 20°C in the case of chickens and Coturnix Quail (Barott and Pringle, 1946; Ricklefs, unpubl.), but body temperature also decreases with decreasing ambient temperature (Fig. 10). Thus neither cooling rate nor metabolism are appropriate for measuring conductance without knowing the temperature gradient. Slopes of the relationship between metabolism and ambient temperature in Rhode Island Red chicks (Table 21) lie very close to the relationship of

TABLE 21

Changes with Age in Thermal and Metabolic Characteristics of Female Rhode Island Red Chickens (after Barrott and Pringle, 1946).

Age (weeks)	0.5	2	5	8	12	18	23	52
Weight (g)	36	90	260	590	1030	1610	1960	2430
BMR (cal/g · hr) at	5.50	6.25	5.95	4.95	3.90	3.10	2.85	2.75
Temperature (°C)	35	35	32	32	29-32	24-27	27	18-24
Slope ¹ (ccO ₂ /g · h · °C)	-0.144	-0.079	-0.056	-0.044	-0.029	-0.021	-0.013	-0.011
Minimum temperature tolerance (°C)	21	21	10	-1	-15	—	—	—
Maximum metabolic rate (cal/g · hr)	12.9	10.85	11	10.8	8.7	—	—	—

¹Slope of the relationship between rate of oxygen consumption and ambient temperature.

conductance to body weight in adults, which may be a significant indication of how galliform chicks manage their energy budgets. Unfortunately, Barott and Pringle (1946) did not present data on body temperatures maintained by the young, so true conductances cannot be calculated. There is no question, however, that the ability of young chickens to regulate their body temperature increases greatly with age.

ENERGETICS OF REPRODUCTION IN BIRDS

INFLUENCE OF TEMPERATURE ON GROWTH

Because ambient temperature affects both the body temperatures and metabolic rates of precocial young, we would expect growth to be affected by ambient temperature as well. If birds are to increase their metabolism with decreasing temperature, they must allocate more energy to the maintenance of body temperature, possibly at the expense of energy available for growth. Reduced body temperature would slow all metabolic processes.

The influence of ambient temperature on the growth of chickens has been experimentally investigated by Kleiber and Dougherty (1934) and Osbaldiston (1966). The most noticeable influence of temperature on growth occurs during the first two or three weeks after hatching. When kept in large groups, chicks grew most rapidly at about 21°C at one week of age; little change in growth rate occurs with temperature thereafter (Osbaldiston, 1966). In fact, over the temperature range 12.8 to 26.7°C, chicks raised in groups exhibited little difference in either food intake or the efficiency with which food was utilized for growth. Singly raised chicks required higher temperatures for rapid growth and temperature clearly influenced growth as late as three weeks after hatching. At low temperatures, chicks consumed more food and used it less efficiently for growth (Osbaldiston, 1966).

Kleiber and Dougherty (1934) analyzed the growth of White Leghorn chicks between 6 and 15 days in somewhat greater detail (Table 22) over the temperature range of 21 to 40°C. Weight gain was most rapid at 21°C (6.5% increase/day) and fell abruptly from 6.1 to 4.6% per day between 32 and 38°C. Even though chicks gained weight most rapidly at 21°C, the energy incorporated into the body reached a peak at 32°C because fat deposition was greater. Most of the weight gain was apparently in tissue growth rather than fat deposition. Why the rate of tissue growth declines slightly between 21 and 32°C is unclear. But the decrease in fat deposition to almost nil at 21°C suggests that the chicks' ability to metabolize energy is limited and that growth (at least fat deposition) and thermoregulatory processes compete. This is consistent with Osbaldiston's (1966) findings that early growth rate declines below about 21°C, and that the huddling behavior of chicks at low temperatures greatly influences their growth rate.

The influence of temperature on growth rate and use of energy, particularly under conditions of temperature, brood size, and parental care that pertain in the wild, should be further explored experimentally. Such studies could help us to understand the development of temperature regulation and parental care in precocial birds and the adaptive significance of brood size in these species.

DEVELOPMENT OF TEMPERATURE REGULATION: ALTRICIAL SPECIES

The young of altricial species are poikilothermic until several days after hatching. The development of thermoregulation has been thor-

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TABLE 22

Growth Performance of White Leghorn Chicks Between 6 and 15 Days as a Function of Temperature (after Kleiber and Dougherty, 1934).

	Air Temperature (°C)					
	21	27	32	38	40	40
Growth rate (% increase/day)	6.5	6.2	6.1	4.6	4.2	4.5
Average weight (g)	74.2	75.4	71.7	65.1	64.0	64.5
Metabolized energy (kcal/day)	42.3	37.8	35.0	26.1	23.3	23.4
Heat production (kcal/day)	35.4	27.4	23.2	17.4	15.9	17.4
Net production (kcal/day)	6.9	10.4	11.8	8.7	7.4	6.0
Average daily:						
weight gain (g)	4.88	4.64	4.39	2.97	2.74	3.09
protein (g)	1.10	1.08	0.97	0.79	0.69	0.67
fat (g)	0.06	0.44	0.67	0.44	0.37	0.24
Standard metabolism						
at 16 days (kcal/bird • day)	20.3	16.5	14.1	11.7	7.2	9.9
(cal/g • hr)	9.9	7.7	7.0	6.7	4.1	5.5

oughly studied from a variety of approaches (Kendeigh and Baldwin, 1928; Kendeigh, 1939; Böni, 1942; Odum, 1942; Dawson and Evans, 1957, 1960; Maher, 1964; Brenner, 1964; Breitenbach and Baskett, 1967; Ricklefs and Hainsworth, 1968; Seel, 1969; Yarbrough, 1970; Morton and Carey, 1971; Diehl and Myrcha, 1973) and a detailed review is not necessary here.

A nestling of a typical small passerine shows signs of a homeothermic response to low temperature within 3-8 days after hatching when placed alone in a temperature chamber. The nestling's capacity for temperature regulation may be quite well developed by 8-15 days, depending primarily on the length of the nestling period of the species (Böni, 1942; Ricklefs and Hainsworth, 1968). Nestlings of large altricial species, including raptors and seabirds, can fully regulate body temperature at a relatively much earlier point in their development than small species (e.g., Dunn, 1973) because large size and growth of a heavy coat of down in most species enhance heat conservation.

Most altricial nestlings can regulate their body temperatures at high ambient temperatures at hatching and their capacity for avoiding heat stress may actually decline with age as conductance and evaporative surface area of the mouth relative to body weight both decrease (Ricklefs and Hainsworth, 1968; Morton and Carey, 1971). Absorption of heat from direct sunlight may be a more critical factor for small

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young than high ambient temperature. Small altricial nestlings have high surface volume ratios and little protective covering of down. Morton and Carey (1971) recount one instance in which three two-day old White-crowned Sparrows (*Zonotrichia leucophrys*) were left unattended in a nest in full sun at high altitude in the Sierra Nevada mountains of California. The young began to pant almost immediately, appeared to be heat stressed within 10 minutes, and were dead within 20 minutes. The authors even suggested that overheating of young in the nest may be a factor causing spontaneous fledging.

Homeothermic capacity is usually measured for isolated birds placed in temperature chambers. This procedure characterizes the development of homeothermy in young but greatly underestimates the ability of a full-sized brood to maintain high body temperatures in a nest. Few studies have been published on cooling rates or metabolic rates of whole broods under normal conditions (cf. Kendeigh and Baldwin, 1928; Royama, 1966; Mertens, 1969). Yarbrough's (1970) comments on the Gray-crowned Rosy Finch (*Leucosticte tephrocotis*) on Amchitka Island, Alaska, are enlightening. Normal ambient temperatures at Amchitka are low and constant (8-10°C); isolated nestlings begin to maintain elevated body temperatures at about 8 days of age, and homeothermy is not strongly developed until 13 days. Yarbrough noted, however, that "A brood of 4-5 young in the nest can regulate its temperature quite accurately at the initial nest temperature from day 3, whereas a single bird cools, even though the nest cup is well-insulated. It may be important to note that in two nests where only three viable young hatched, these young were also dead and the nests abandoned before day 8." Since the strategies of development and parental care are optimized with respect to temperature and metabolic characteristics of young in the nest, not their performance under standard conditions, further study in this area is greatly needed.

Development of homeothermy has been related to several factors that influence the ability of the young to produce and conserve heat: (1) decreasing surface/volume ratio with increasing size, (2) increasing insulation with the development of contour feathers, and (3) increased capacity to produce heat with growth and maturation of the major skeletal muscle masses. Whether the developmental course of homeothermy is an important component of the growth strategy or whether it is merely a consequence of other more important aspects of development is not known.

Most species show signs of homeothermic response before contour feathers break through their sheaths and provide any substantial degree of insulation. This led Dawson and Evans (1957, 1960) to emphasize the role of surface/volume ratios in their discussion of the ontogeny of thermoregulation. But among passerine species weighing less than 100 grams, development of homeothermy is related primarily to the length of the nestling period independent of body weight growth (Ricklefs and Hainsworth, 1968). Thus heat generation capacity and

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insulation also must exert important influences on the development of temperature regulation.

Insulation, or its inverse, conductance, can be estimated from cooling rates of poikilothermic young, although metabolic heat production, especially by older young, causes values for conductance to be underestimated. Conductances calculated from cooling rates for live Starling and Gray-crowned Rosy Finch nestlings (Fig. 12) indicate that insulation increases very little beyond that afforded by the body itself until the young approach adult weight. The rapid drop in the apparent conductance (not corrected for metabolism; see Bartholomew and Tucker, 1963) after eight days in the rosy finch must be largely caused by the rapidly developing homeothermic metabolic response. Three- to eight-day old rosy finch nestlings lose heat more rapidly than defeathered adult birds (Herreid and Kessel, 1967) apparently because of peripheral circulation of blood, especially to the developing feather sheaths in live birds (Yarbrough, 1970). On the other hand, Kendeigh and Baldwin (1928) found that the temperature of dead 3- and 5-day old House Wrens decreases about 1.5 times faster than that of live birds. They suggested that live birds appear to lose heat less rapidly than dead young because part of the heat loss is replaced by metabolic heat production. Wrens do not begin to develop feather sheaths until considerably later than rosy finches, however, and heat loss of live wrens may increase at a later age.

The conductances of nestling Starlings, calculated by the method shown in Figure 5, are about twice those of the Gray-crowned Rosy Finch because metabolic heat loss was included in the total. All the measurements were made on birds less than 11 days of age, before body feathering had progressed far, completely exposed to ambient air in cheesecloth bags. That the conductance of young starlings exceeds that of skinned adults attests to the poor insulative value of skin and the role of blood circulation in carrying heat to the body surface.

Breitenbach and Baskett (1967) measured the temperature decrease of living and dead nestling Mourning Doves exposed to 2°C. Even at three days of age, the conductance of young doves was considerably lower than that of Starlings and rosy finches, indicating development of some insulation at an early age. But small brood size (2) and flimsy nest construction in doves probably more than offsets any greater capacity for heat conservation in the young. At three and six days, cooling rates of live birds were greater than those of dead birds, despite metabolic heat production. This difference is almost certainly caused by peripheral circulation to developing feather sheaths.

Heat for temperature regulation in nestling birds is derived almost entirely from shivering (West, 1965). The onset of homeothermy is closely paralleled by the appearance of shivering. In the House Wren shivering is absent in 3-day old birds but does occur in 6-day old birds (Odum, 1942; Table 23). Morton and Carey (1971) observed shivering

TABLE 23
Developmental Course of Shivering in Nestling House Wrens (after Kendeigh, 1939, and Odum, 1942).

	Age (days)																		
	0			3			6			9			12			15			Adult
Body temperature (°C) ¹	21.1			22.2			24.4			27.8			36.7			38.9			40.6
Feather length ¹ (mm) ²	0			0			1			5			9			12			16
Function ³	T	P	M	T	P	M	T	P	M	T	P	M	T	P	M	T	P	M	
Air temperature (°C)																			
40.6	1.8			2.0			2.4			2.9			3.3			3.6			4.6
37.8	1.6			1.9			1			5			3			4			7
35.0	1.4			1.9			3			7			7			3			8
32.2	1.0			1.8			17			16			21			8			28
26.7	0.6			1.0			29			30			34			30			95
21.7	0			0.3			0			2.8			35			34			100
				0.6			1.3			2.8			35			6.2			4

¹When exposed to an air temperature of 21.7°C (about 70°F).

2. Average length of contour feathers, from Boulton (1927).

³T = number of tremors per second; P = percent of time tremors present; M = metabolic rate (cc CO₂/g · hr).

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in 39% of 4-day old birds exposed to temperatures below 30°C. The shivering response, measured by the number of muscle tremors per second and the percent of time tremors occur at a particular temperature, is as well developed in 6-day old House Wrens as it is in nestlings ready to fledge (Table 23). Thus, the neurophysiological basis of temperature regulation appears to be fully developed at an early age. The development of full homeothermic capacity must, therefore, be delayed by the slow acquisition of insulative plumage, and the relatively small weight and slow maturation of skeletal muscle in small young (Ricklefs, 1967, 1974). Development of homeothermy thus appears to be tied closely to the maturation of skeletal muscle for locomotion. Without a well-developed capacity for heat production, no amount of insulation would permit maintenance of a constant body temperature.

The absence of homeothermy in young altricial nestlings is, of course, compensated for by the brooding behavior of the adults. Temperatures of newly hatched passerine birds are maintained within a range that is similar to that of incubated eggs, generally 34-36°C (for examples, see Stoner, 1945; Kendeigh and Baldwin, 1928; Ricklefs and Hainsworth, 1969; Morton and Carey, 1971; Gotie and Kroll, 1973). Body temperatures of young in undisturbed nests are rarely allowed to fall below 30°C, and may be as high as 39°C in very young birds while they are being brooded. The normal range of nestling body temperatures increases and becomes more narrowly regulated as the young grow. Body temperatures of nestling Cliff Swallows average 35.3, 39.1, 41.2 and 42.2°C on the 1st, 5th, 10th and 20th days after hatching (Stoner, 1945). This basic pattern of temperature development occurs in tropical regions (unpublished data) and in Arctic regions as well. Kendeigh and Baldwin (1928) found that the drop in body temperature of nestling House Wrens during the female's normal inattentive period at ambient temperatures of 10-20°C was about 2.5-3°C just after hatching and had decreased to less than 1°C by the sixth day.

Body temperatures of the young of nonpasserine altricial species have been studied less frequently. Bartholomew and Dawson (1954) found that in the absence of parental brooding body temperatures of naked young Brown Pelicans in the Gulf of California varied widely with ambient temperature and insolation. Daytime temperatures were 24-27°C and nighttime temperatures were 16-17°C; body temperature extremes of 21.4-43.7°C were observed. By the time the young acquired their downy plumage the body temperature range narrowed to 37.8-41°C. In the same study young Great Blue Herons (*Ardea herodias*) could regulate their body temperatures better than pelicans at low ambient temperatures and exhibited a diurnal range of 32.2-43.5°C. Temperatures of small (less than one week old) Western Gulls (*Larus occidentalis*) did not fall below 34.6°C.

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YOLK RESERVES OF NEWLY HATCHED YOUNG

Eggs of precocial species contain more energy per unit of volume than the eggs of altricial species, primarily because of their high lipid levels (Table 9). Additional energy may be stored in the egg partly to offset the somewhat higher respiratory rate and longer period of embryonic development in precocial birds, but a substantial portion of the yolk reserve is available to the chick after hatching. On the basis of embryonic metabolism measurements of Kashkin (1961), Romijn and Lokhorst (1960), and Kendeigh (1963), Drent (1970) estimated that embryos of the domestic duck and domestic chicken used only about 40% of their fat stored during the embryonic period, whereas House Wrens consume virtually all of the fat provided in the egg. Drent's estimate for the Herring Gull, based on his own work is in error because he calculated the proportion of lipid in the egg from data on chickens (67% lipid). Drent's data on the caloric value of the dried egg contents suggest that the proportion of lipid in the egg is closer to 33%, of which the embryo uses about 89%.

Young are hatched with varying amounts of lipid reserves which occur in fat deposits and as unassimilated yolk. Fat deposits are rarely measured in neonates and so yolk content must be used as an index of the minimum energy reserves available to the newly hatched chick. Most passerines have relatively little yolk left at hatching, between 5 and 10% of their body weight according to Schmekel (1961). Galliform birds may have considerable yolk reserves with the amount varying from 10% of yolk-free body weight in the Bobwhite to 25% in White Holland Turkeys (Romanoff, 1944; Marcstrom, 1966). Anseriform hatchlings also have substantial yolk reserves, 10-16% in the Mallard (Kear, 1965; Marcstrom, 1966) and 22% in the Embden Goose (Romanoff, 1944). Yolk reserves of three species of *Calidris* sandpipers at hatching is 5-7% (Norton 1973) and must be even lower for Herring Gulls. Among altricial nonpasserine species, Double-crested Cormorant (*Phalacrocorax auritus*) chicks removed from pipped eggs contained 16% yolk (Dunn, 1973). Yolk reserves of hatchlings appear to be correlated with the yolk supply of the freshly laid egg, but they do not seem to be related to whether the young develop altricially or precocially.

In the domestic chicken the yolk reserve of the newly hatched bird may function as much as a protein supply as an energy source. The yolk of the neonate is about 57% dry material (compared to 51% in the fresh egg yolk), but the dry weight is only 30% lipid (compared to 63% in the fresh egg) (Romanoff, 1944). If the diet of young chickens contains a large proportion of vegetable material with low protein content, or if it is deficient in overall amount, protein stores would be needed during the first few days after hatching to support rapid tissue growth. The yolk of neonates of another galliform species, the Capercaillie (*Tetrao urogallus*), is 53.4% dry material, of which 55% is lipid

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(Marcstrom, 1960). Thus the yolk of the newly hatched chick more nearly corresponds to that of the fresh egg in the Capercaillie than it does in the chicken. The yolk of newly hatched mallard ducklings contains only 36% dry substance (Kear, 1965), but proportions of lipid and protein have not been analyzed. On the other hand, the body of the newly hatched mallard contains 35% lipid (excluding yolk) compared to 28% for the Capercaillie (Marcstrom, 1966). In both cases most of the energy reserve is in the form of body fat, not in the yolk sac. The total lipid reserves (including yolk) of the newly hatched White Leghorn chick are about 12% of the body weight and the lipid is about equally distributed between the yolk sac and the body (Romanoff, 1932). Most species apparently use most of their yolk reserves at a fairly even rate over the first 4 or 5 days after hatching (Romanoff, 1944; Marcstrom 1960). In the chicken, yolk is assimilated at the rate of about 1 gram dry weight per day which represents 5.9 kcal/g of metabolizable energy. This would supply most of a 1-day old White Leghorn's basal metabolic rate of 6.8 kcal/day (Medway and Kare, 1957). Yolk reserves thus apparently give the newly hatched chick substantial energetic independence, allowing the bird an opportunity to get on its feet before having to meet all of its energy needs by its own foraging. In Mallard ducklings the yolk reserve is used almost completely within the first two days after hatching, although some of the material in the yolk is apparently transferred to the liver (Kear, 1965).

ACCUMULATION OF ENERGY WITH GROWTH

The energy requirements of growing birds include a component that represents maintenance energy requirements and the work of biosynthesis, which may be measured by respiratory gas exchange, and a component that represents the accumulation of energy in body tissues and fat stores, which may be measured by carcass analysis. The rate of accumulation of energy in the body can be estimated by multiplying the rate of weight gain by the energy density of the body (kcal/g wet weight). Energy density has been found to increase with age in most species, largely because the water content of tissues decreases but partly because lipid levels increase in many species (Ricklefs, 1967). It will be convenient, for the purpose of constructing models of the growth process, to relate energy density to percent of adult weight attained (as in Fig. 13) rather than to age. For most species, the relationship between live-weight energy density and percent adult weight can be adequately described by a linear equation of the form

$$D = a + bW$$

where D = energy density (kcal/g wet weight),

a = Y-intercept, which may be interpreted as energy density at weight 0,

W = proportion of adult body weight attained, and

b = slope of the linear relationship.

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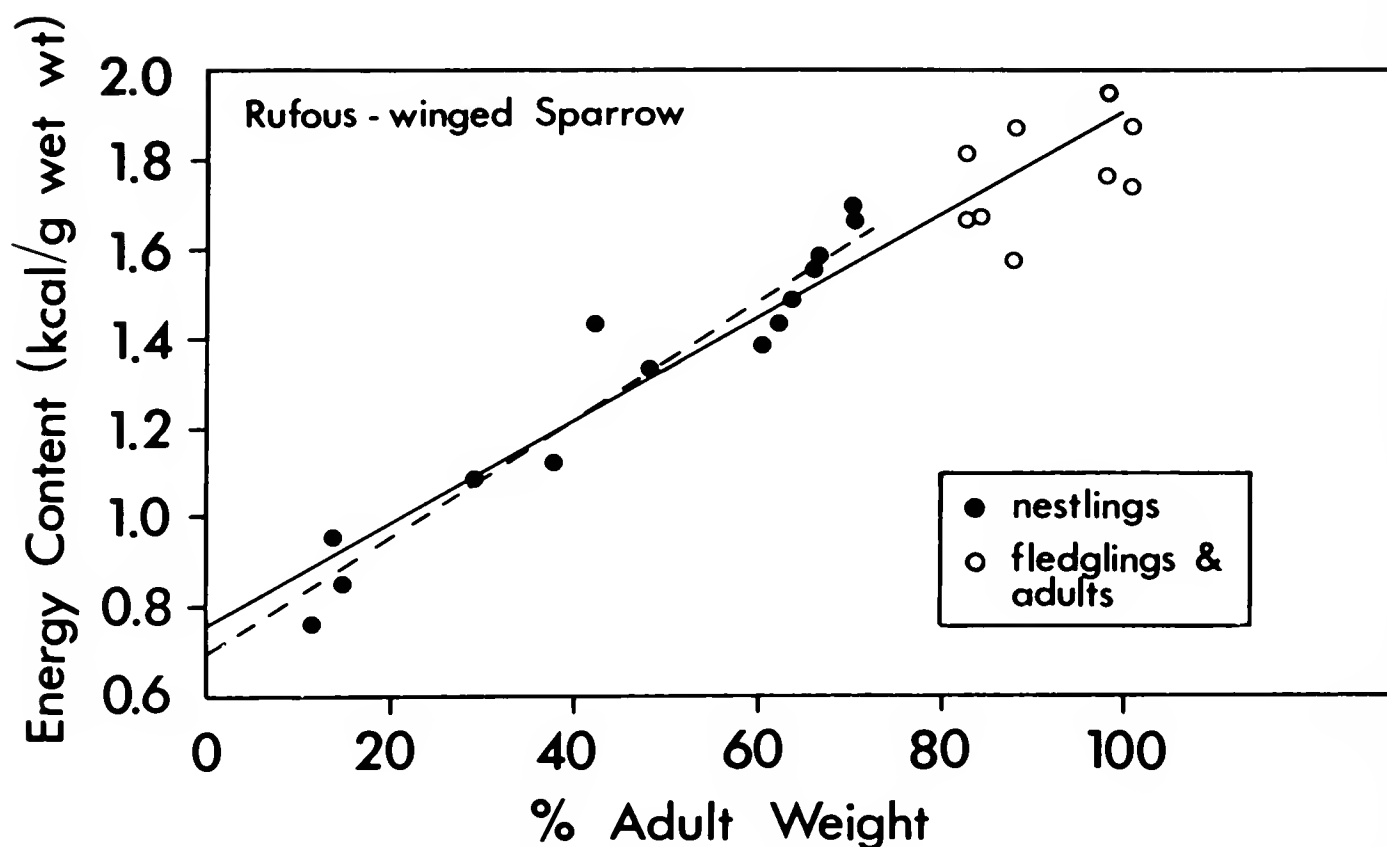


FIG. 13. Energy content of Rufous-winged Sparrows (kcal/g wet weight) as a function of percent of adult weight attained. Regressions are plotted separately for nestlings (solid circles) and for the entire series, including fledglings and adults (open circles) (Ricklefs and Austin, unpubl.).

For the Rufous-winged Sparrow (Fig. 13) the equation is $D = 0.69 + 1.31 W$ for nestlings (up to 75% adult body weight), or $D = 0.76 + 1.14 W$ for a more extensive series including juveniles and adults.

Changes in energy density during development in a variety of species (Table 24) suggest several characteristic patterns. Altricial species (passerines, dove, cormorant) have low initial energy densities (a 0.5-0.8 kcal/g), owing to the high water content of tissues in altricial birds at hatching. But energy density increases rapidly with growth (slope = 1.0-1.6). The relatively great slope of the cormorant and Ring Dove (1.53, 1.61) are probably due to a high rate of fat deposition.

Precocial species possess relatively mature tissues with low water content at hatching and thus their intercept (a) is generally high. But because the body composition of adult precocial and altricial species does not differ considerably, species with high values of a have correspondingly low values of b (Fig. 14). Ranking "precocial" species in order of increasing precocity by these criteria yields the following arrangement: Common Tern, Coturnix Quail, Sooty Tern (*Sterna fuscata*), Dunlin, and White Leghorn chicken. Leach's Petrel has a high intercept related to extremely precocious development and a steep slope caused by extensive fat deposition (Ricklefs, White, and Cullen, unpublished). This pattern also appears, but most weakly, in the chicken. I am also struck by the apparent precocity of development, using energy density as the criterion, in the Dunlin compared to terns. This should emphasize that most descriptive terms applied to mode of development are narrowly defined and are not adequate for general comparative purposes.

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TABLE 24

Relationship of Energy Density (kcal/g wet weight) to Proportion of Adult Weight Attained by Growing Birds.

Species	n ¹	r	a	b	Reference
Leach's Petrel	32	0.86	1.87	1.50	Ricklefs, White, and Cullen, unpubl.
Double-crested Cormorant ²	—	—	0.71	1.53	Dunn, 1973
Coturnix Quail	16	0.89	1.05	1.33	Ricklefs and Cullen, unpubl.
White Leghorn Chicken	8 ³	0.95	1.58	0.86	Medway and Kare, 1957.
Common Tern	24	0.91	0.92	0.96	Ricklefs and Cullen, unpubl.
Sooty Tern	25	0.75	1.29	0.68	Ricklefs and White, unpubl.
Dunlin	—	—	1.50	0.30	Norton, 1970
Ringed Dove	5 ³	0.99	0.75	1.61	Brisbin, 1969 ⁴
Mourning Dove	20	0.92	0.92	1.05	Ricklefs, unpubl.
Barn Swallow (15 days)	33	0.92	0.63	0.99	Ricklefs, 1967
Long-billed Marsh Wren ²	4 ³	0.94	0.51	1.32	Kale, 1965
Cactus Wren ²	34	0.91	0.69	1.11	Ricklefs, 1974
Red-winged Blackbird ⁴	22	0.89	0.78	1.11	Ricklefs, 1967
Rufous-winged Sparrow nestlings	14	0.97	0.69	1.31	Ricklefs and Austin, unpubl.
whole series	23	0.96	0.76	1.14	

¹ n = number of individuals; r = correlation coefficient of regression; a = y -intercept; b = slope of regression.

² Nestlings only.

³ Pooled samples.

⁴ Data taken from graphs.

Most of these values are the result of extensive recalculation of original data. Basic information is usually fat weight and lean dry weight corrected for ash content; energetic equivalents used were 9.0 and 5.5 kcal/g, respectively.

METABOLISM DURING THE GROWTH PERIOD

Metabolic rate includes costs of maintenance and costs of biosynthesis. Metabolism is most commonly estimated as the uptake of oxygen in either an open or closed system measured by electrodes or magnetic devices sensitive to changes in the partial pressure of oxygen. Gravitimetric measurement of carbon dioxide output and volumetric measurement of oxygen consumption have been used extensively in earlier

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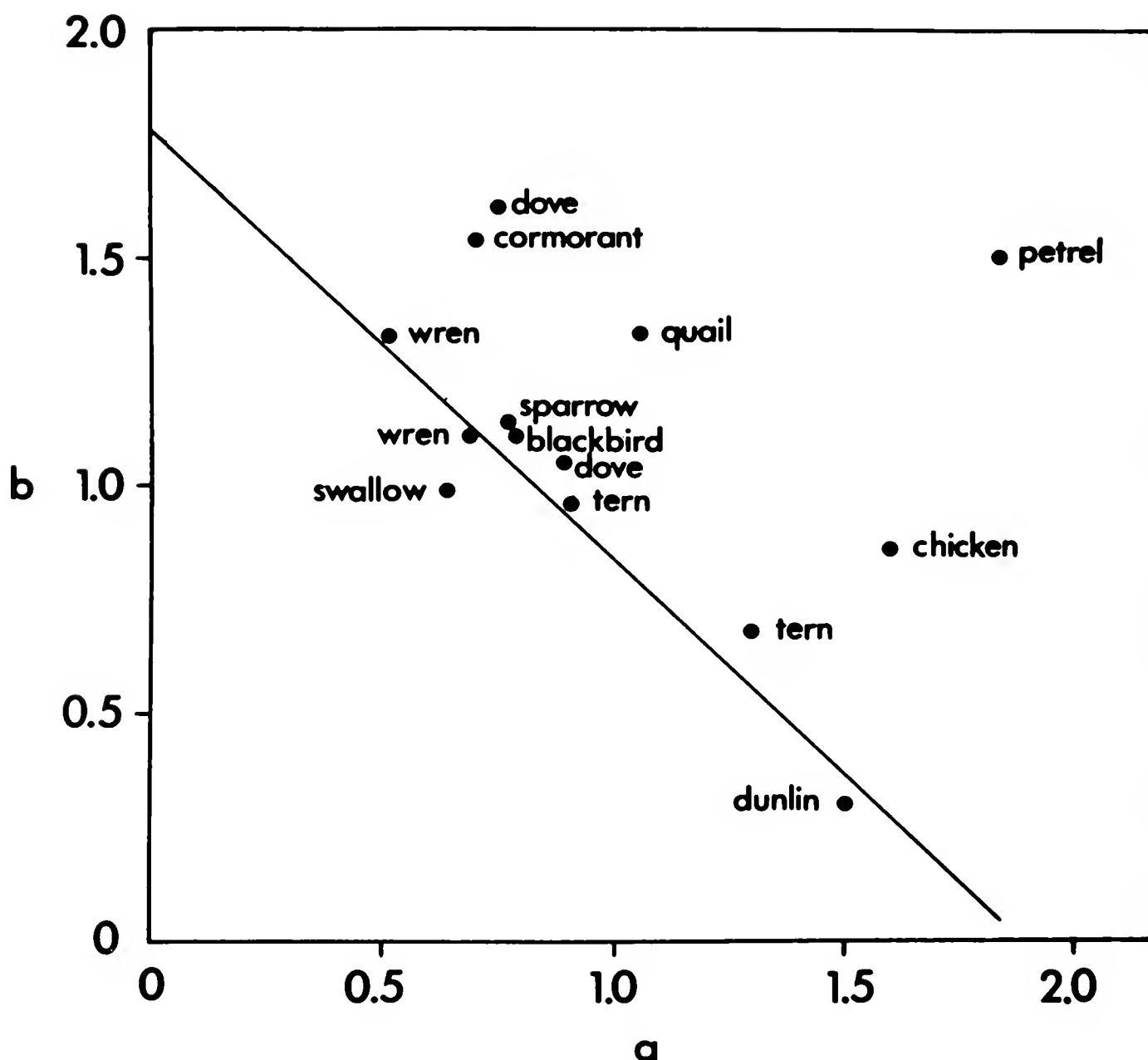


FIG. 14. Relationship between the parameters a and b in the equation $\text{cal/g wet weight} = a + b$ (proportion adult weight). Values are from Table 24. Line suggests the relationship between a and b for species that store little fat during the development period.

studies, particularly when metabolic rate is low. Oxygen consumption may be converted into energetic equivalents if the respiratory quotient (R.Q.) is either measured or estimated (see below).

The metabolism of young birds is most commonly measured under so-called "standard" conditions. This practice affords a useful index of development of the young, as does the ability of young to regulate their body temperatures under metabolism chamber conditions, but in species with well-insulated nests and large broods such predominately physiological techniques have limited bearing on primarily ecological problems. The natural metabolic rates of young that develop with siblings in nests are poorly known (see, however, Myrcha, Pinowski and Tomek, 1970, 1972; Diehl and Myrcha, 1973; and Westerterp, 1973) and have been studied experimentally with respect to brood size only by Royama (1966) and Mertens (1969), both working with the Great Tit, and Brisbin (1969), working with Ringed Doves.

Oxygen consumption, usually expressed as $\text{cc/g}\cdot\text{hr}$, is the most frequently used measure of metabolism. Formulae for calculating energy

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expenditure from oxygen consumption and respiratory quotient were presented on page 158. Under post-absorptive conditions, one usually assumes that fat is the primary source of energy and that R.Q. is close to 0.7, for which the energetic equivalent of oxygen consumption is about 4.7 cal/cc O₂. In fact, the respiratory quotient of fasting birds is usually greater than 0.7 just after hatching and decreased with age. For example, the R.Q. of fasted White Plymouth Rock chickens from hatching to six weeks of age varied widely between 0.73 and 0.90, but was between 0.68 and 0.73 in birds older than 10 weeks (Mitchell, et al., 1927). The R.Q. of European Tree Sparrows declined from almost 1 on days 1 and 2 to 0.75 at the end of the nestling period (Myrcha, Pinowski and, Tomek, 1970). Dyer (1968) reported a similar decrease in R.Q. during the nestling period in the Red-winged Blackbird (*Agelaius phoeniceus*).

Changes in metabolic rates of young birds during development fall between two extreme patterns. On the one hand, altricial species, exemplified by passerines, initially have low basal metabolic rates compared to adults on a per gram basis. The metabolic rate then increases during the development period and usually exceeds the adult level before fledging (Fig. 15). On the other hand, the basal metabolic rate of a typical precocial species increases to a peak soon after hatch-

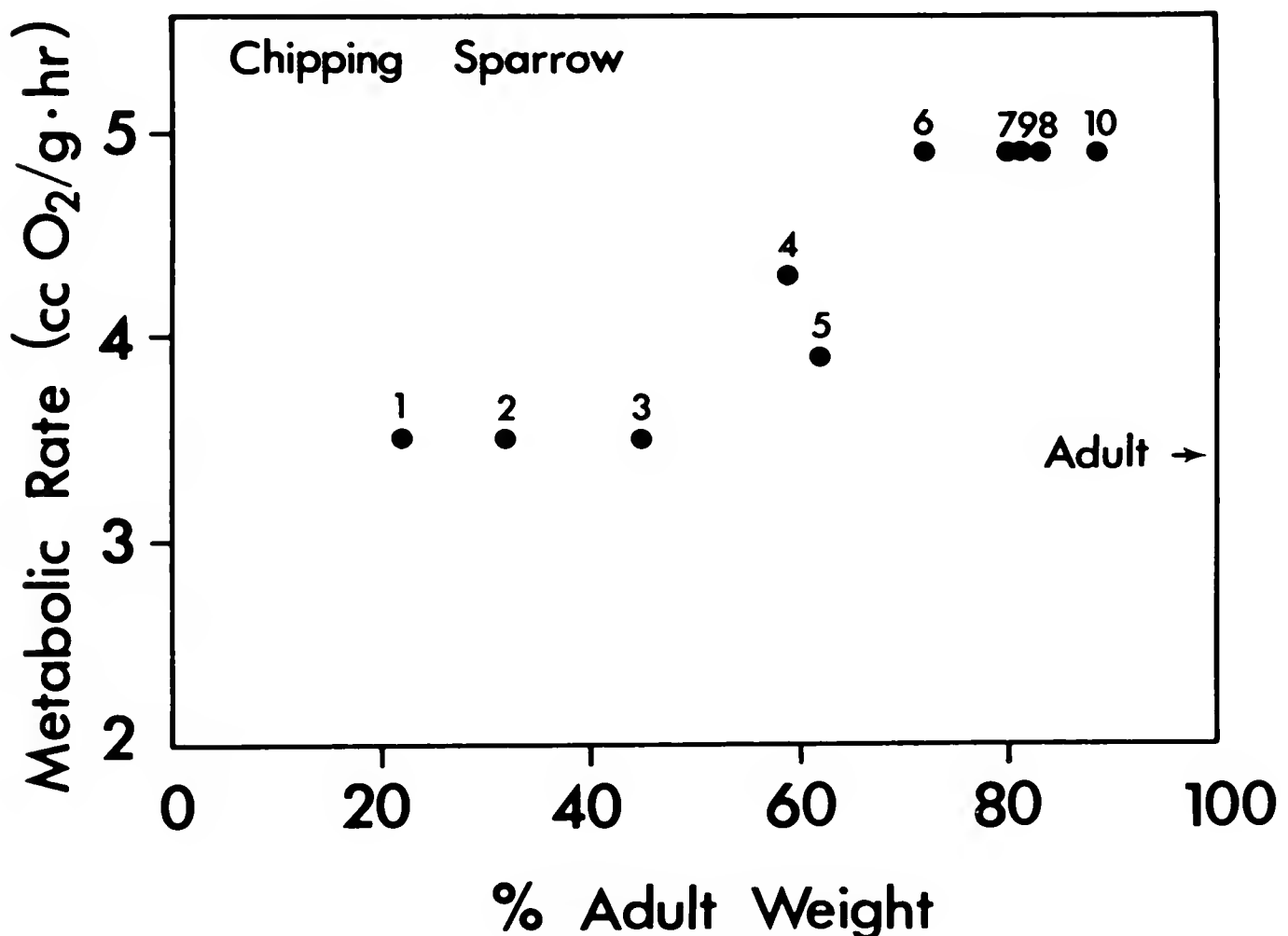


FIG. 15. Metabolic rate of Chipping Sparrow nestlings at 35°C as a function of proportion of adult weight (12.2 g). Ages, in days, are indicated by numerals. Adult metabolism, calculated from the equation for resting adult passerines in Aschoff and Pohl (1970), is indicated by the arrow. Data taken from a graph in Dawson and Evans (1957).

ing and then gradually declines to the adult level with growth (Figs. 16 and 17).

Dawson and Evans (1957) suggested that the metabolic rates of nestling altricial birds increase to adult levels during development, but do not rise substantially higher. For example, the metabolic rate of House Wrens was less than 50% of adult level during the early part of the nestling period, based on Kendeigh's (1939) data. In fact, most passerine young appear to use energy at about the same level as, or a little lower than, adults on a per gram basis shortly after hatching. The energy requirement increases to a varying amount above the adult level during the nestling period (e.g., Fig. 15). My interpretation of metabolic changes with growth differs slightly from that of Dawson and Evans, partly because they used the Brody-Procter equation to estimate adult metabolism and I have used the Aschoff-Pohl equation for resting birds. For the Chipping Sparrow (*Spizella passerina*) (adult weight = 12.2 g) these values are 3.85 and 3.4 cc O₂/g·hr, respectively. The metabolic rate of older nestlings at 35°C, 4.9 cc O₂/g·hr, is 44% above the Aschoff-Pohl adult level, but only 27% above the Brody-Procter levels. Dawson and Evans' measurements on sparrow nestlings were made within a few hours of the birds' last feeding and, therefore, may be higher than most measurements on adults under truly standard conditions, because of residual specific dynamic action. The basal metabolic rate of adult Chipping Sparrows may also differ considerably from the Aschoff-Pohl prediction. Kendeigh's (1939) data for the House Wren are somewhat confusing; his basal metabolic rate of adults is considerably higher than the Aschoff-Pohl prediction; if Kendeigh's value is incorrect it would cause the metabolic intensity of the young to appear low (see Dawson and Evans, 1957). Too few comparative data are available for species under standardized conditions to determine whether changes in metabolic rates of passerines exhibit a typical form or whether they vary with respect to such factors as length of nestling period.

The metabolic intensity of precocial chicks rises rapidly, often to several times adult level, soon after hatching (Fig. 16). This pattern coincides with the rapid increase in locomotor and thermoregulatory capacity evident in young of this type soon after hatching. Metabolic rates of newly hatched domestic chickens (1-3 days) are about twice that of full-term (19-20 day) embryos (Mitchell, et al., 1927), and increase steadily during the first two weeks, even though chicks may not show any weight gain. The early increase in metabolism is caused by fundamental physiological changes that occur early in post-hatching development but which are not specifically related to growth.

The developmental course of metabolic rate in the Dunlin is similar to that of the chicken (Fig. 17), but the relationship of this pattern to the precocial mode of development is somewhat obscured by its additional occurrence in the Pigeon Guillemot (Fig. 18) and its rather weak expression in Sooty terns (Fig. 19).

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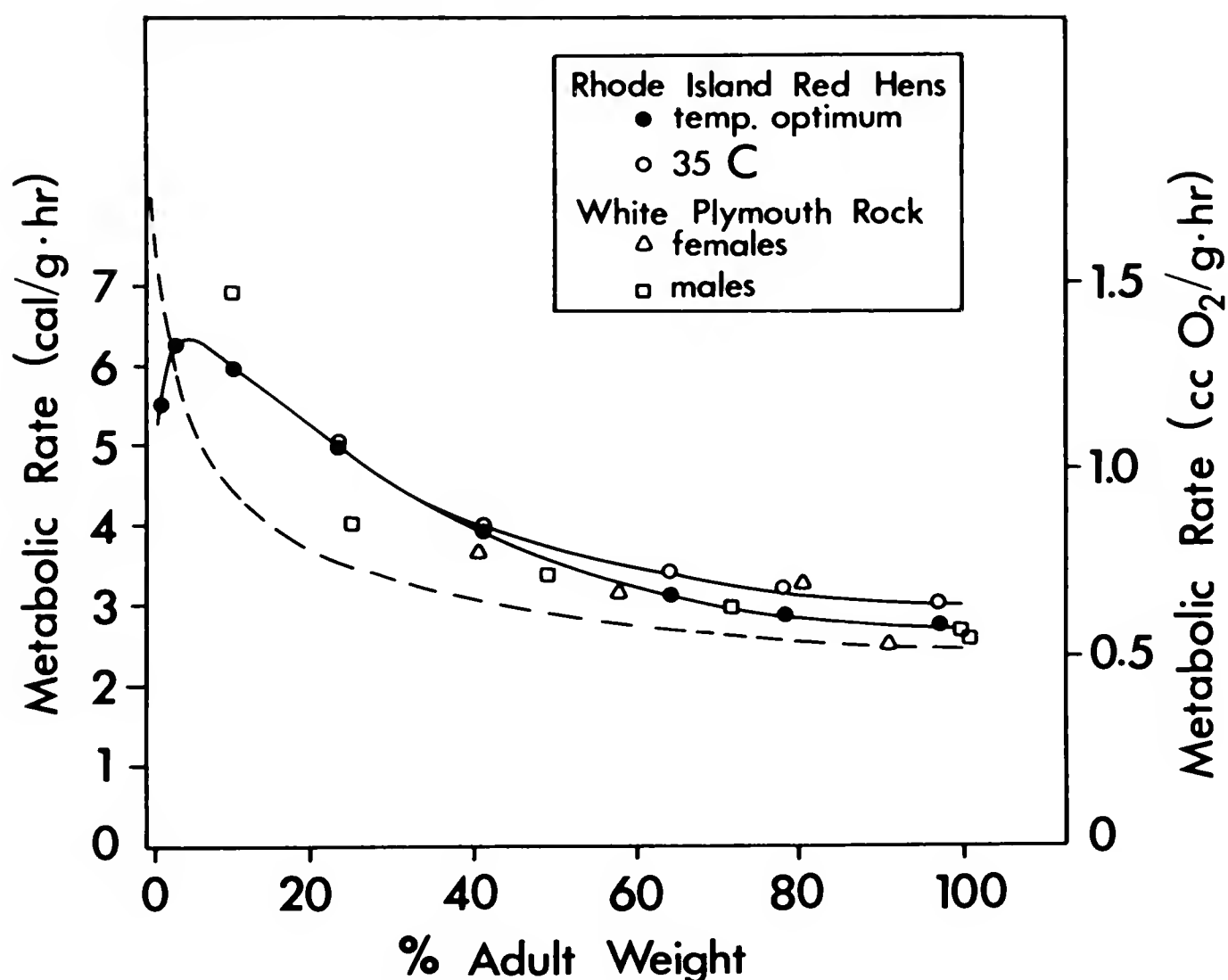


FIG. 16. Metabolic rate of Rhode Island Red hen chicks at 35°C, and at the temperature of minimum metabolism, as a function of proportion of adult weight (2,500 g) attained (data from Barrot and Pringle, 1946). Values for White Plymouth Rocks (adult weight: males, 2,700 g; females, 1,800 g) are included for comparison (data from Mitchell, et al. 1927). Dashed line represents the Aschoff Pohl (1970) equation for inactive, adult nonpasserines.

Pigeons and doves exhibit an apparently unique pattern of change in basal metabolic rate as a function of age (Fig. 20). Metabolic rate is initially 2-3 time adult level, as it is in precocial species, but it remains high until the young have attained more than one-half adult body weight.

COMPONENTS OF METABOLISM

One can estimate the contribution of biosynthetic work to the energy expenditure of the chick if one knows the growth rate and weight specific energy content of the body. The difference between total energy expenditure, measured by gas exchange, and the work of biosynthesis is the maintenance metabolism of the chick.

The growth rate of a bird at any particular point on the growth curve, from 0 to 100% of adult weight attained, can be calculated from equations fitted to growth data (Ricklefs, 1967a, 1968, 1969). The growth curves of most species of birds can be reasonably approximated by either the logistic equation (most passerines, raptors, and rapidly growing seabirds) or the Gompertz equation (most precocial species

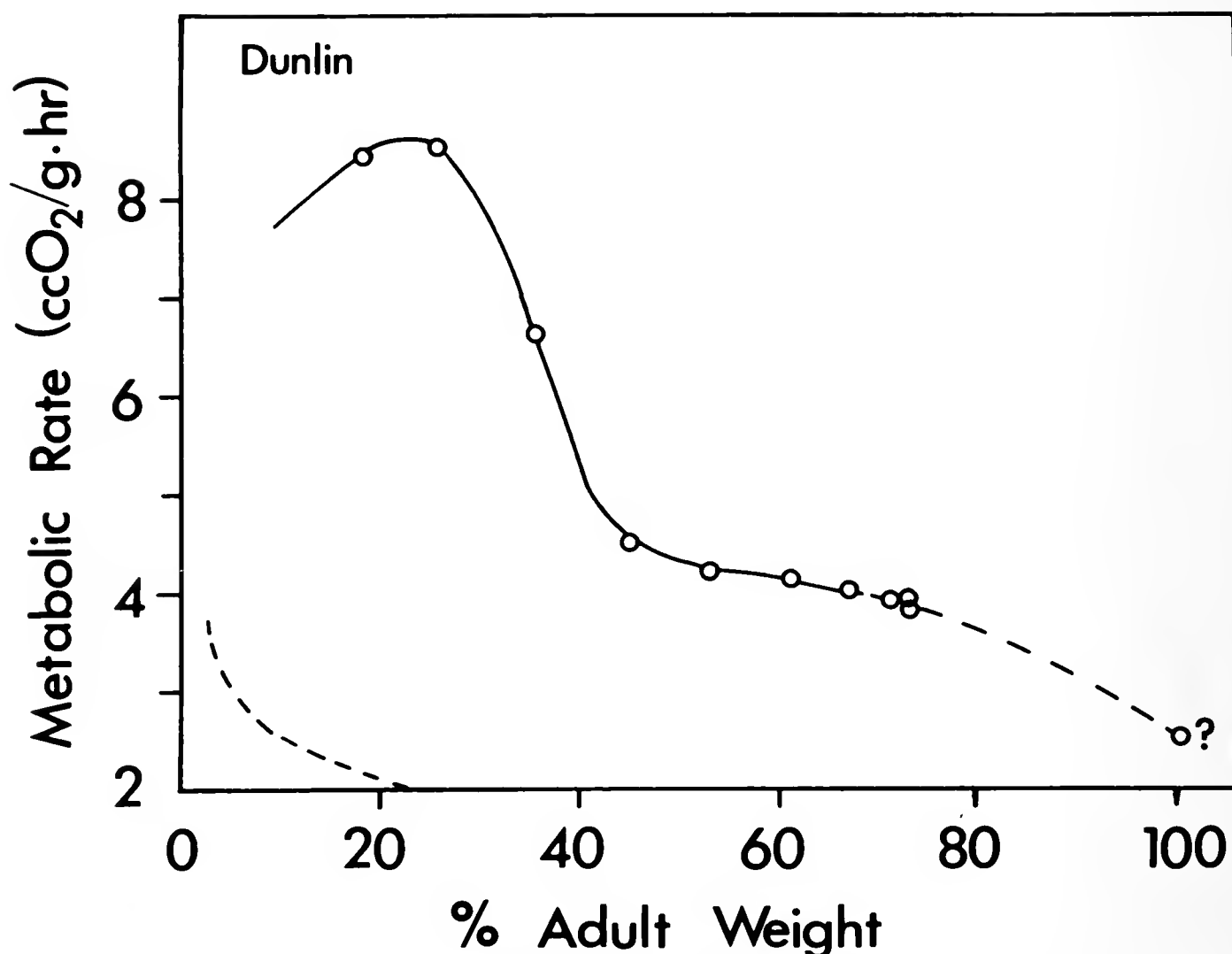


FIG. 17. Metabolic rate of Dunlin chicks at 35°C as a function of percent of adult weight (57.5 g; from graphs in Norton, 1970). Dashed line represents adult metabolism calculated from equation for resting nonpasserines in Aschoff and Pohl (1970). The oxygen consumption of a full-term (8 g) embryo at 38°C was 2.25 ccO₂/g·hr.

and seabirds). The absolute rate of increase (dW/dt), according to the logistic equation, is

$$dW/dt = KAW (1 - W)$$

where W is the proportion of the asymptote of the growth curve attained, A is the asymptote, and K is the growth rate constant. For the Gompertz equation,

$$dW/dt = -KAW (\log_e W)$$

Maintenance metabolism is calculated for White Leghorn chickens of different body size in Table 25. The growth curve of this bird can be fit by a Gompertz equation with an asymptote (A) of 1,800 g and growth rate constant (K) of 0.024. For a White Leghorn chick that weighs 30% of the asymptotic ($W = 0.3$), total energy expenditure is 63.50 kcal/day (4.9 cal/g·hr (see Table 25) \times 24 hours \times 0.30 \times 1800g \div 1000). The growth rate (dW/dt) is 15.6 g/day ($-0.024 \times 1800 \times 0.3 \times \log_e (0.3)$) which, with an energy density of 1.87 kcal/g wet weight (calculated from equation in Table 24), is equivalent to a tissue and fat accumulation of 29.18 kcal/day. Assuming a production efficiency of 75% (see page 170), 9.73 kcal/day ($29.18 \div 3$) must be

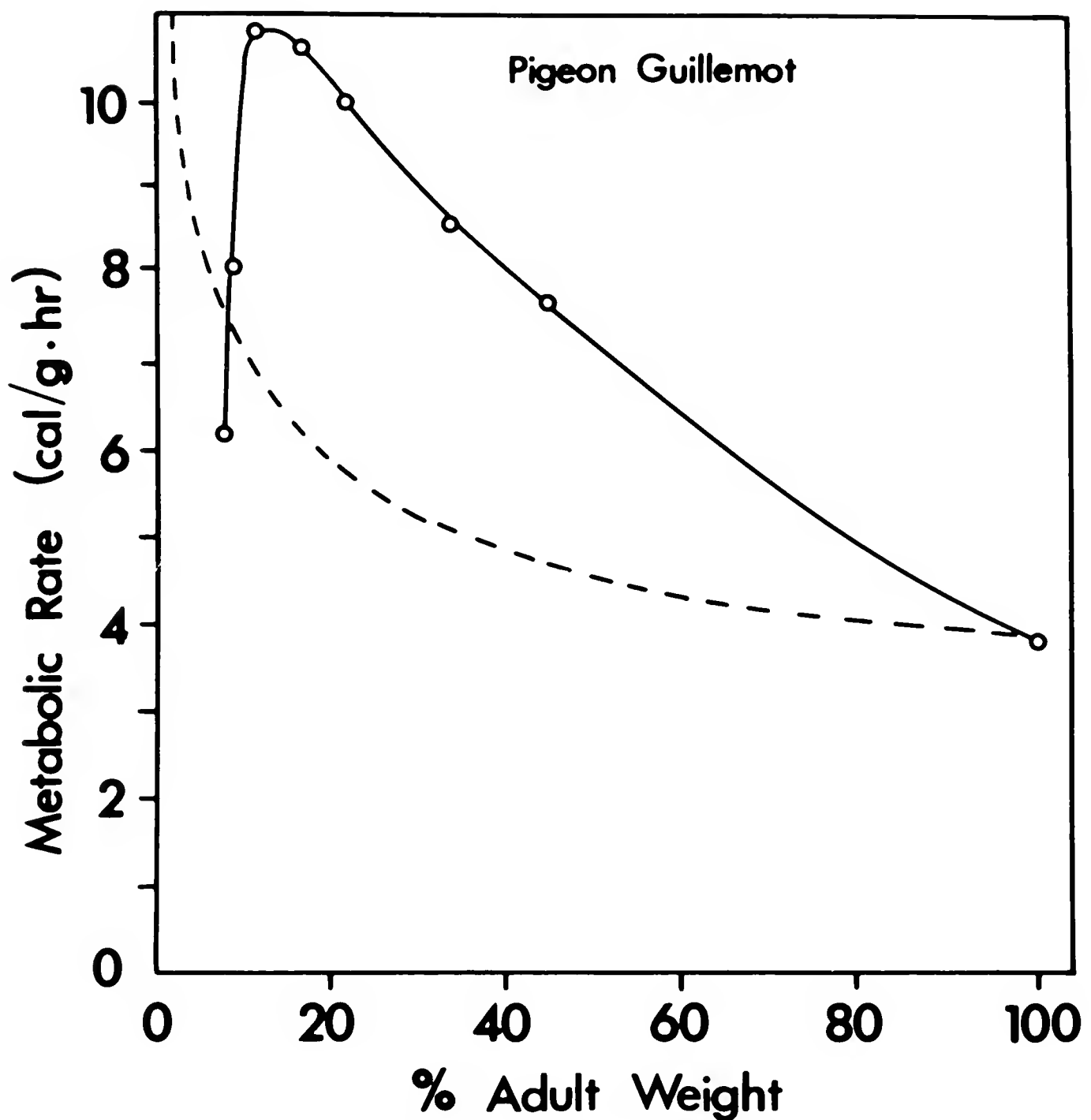


FIG. 18. Metabolic rate of Pigeon Guillemot nestlings in their thermoneutral zone as a function of percent adult weight attained (450 g). The Aschoff-Pohl (1970) prediction for inactive, nonpasserine adults is indicated by the dashed line. Data from Drent (1965).

expended to support the work of biosynthesis, leaving 53.77 kcal/day (63.50-9.73) as the expenditure for maintenance. This is equivalent to an expenditure of 4.15 cal/g·hr, or about 15% less than the measured metabolic rate. In slowly growing precocial species, correcting metabolism rate for the work of biosynthesis does not alter the overall pattern of energy expenditure as a function of growth (Fig. 21). Similar calculations for a rapidly growing passerine indicate that up to 40-50% of the energy expenditure by the nestling during the first few days after hatching may represent the work of biosynthesis.

If precocial young were as capable of maintaining themselves as adults of similar size, we might expect the metabolic rate of the young during the growth period to follow the metabolic rate-body size relationship observed for adults. In fact, metabolic rates of precocial young exceed the predicted adult rate for their size early in the growth

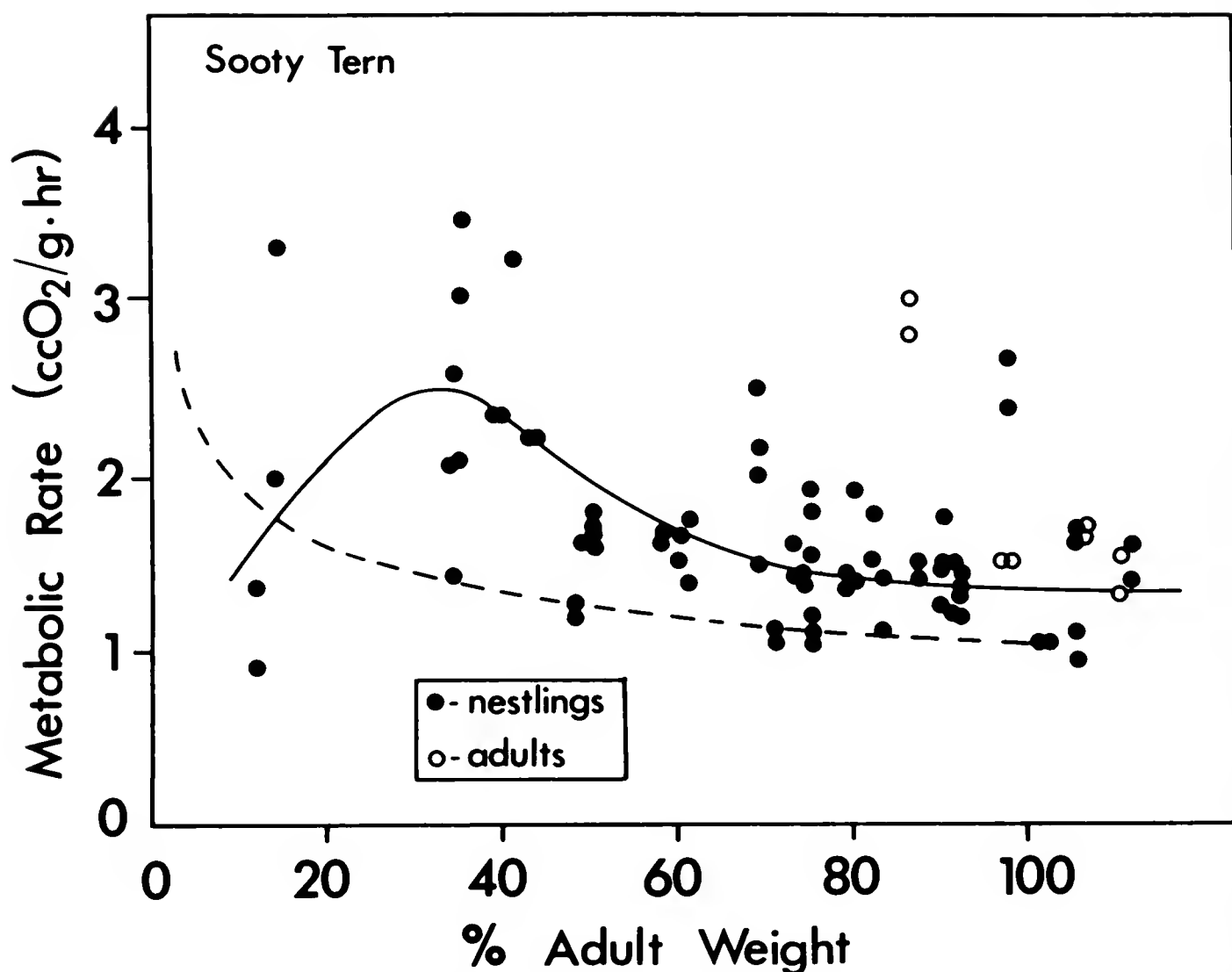


FIG. 19. Metabolic rate of Sooty Terns at prevailing ambient temperatures (20-30C), and under natural nutritional conditions, as a function of proportion of adult weight (175 g). Observed rates for adults are about 50% greater than the Aschoff-Pohl prediction (dashed line). Unpublished data of Ricklefs and White.

period and remain above the adult curve almost until adult weight is attained (Fig. 21). Altricial species differ from precocial species primarily in that the expected adult metabolic rate is exceeded only after the young attain a greater proportion of adult body weight (Figs. 15 and 22).

I do not know why basal metabolic rates of growing birds exceed those of adults of similar size. Estimates of maintenance energy may be incorrect, but the discrepancy between observed and predicted metabolic rates seem too great to be accounted for by error of measurement. Since we do not understand the meaning of basal metabolism in general, it is not surprising that we may find the solution to a more specialized developmental problem elusive. We know from empirical measurements that the ratio between basal metabolism and maximum work output is nearly constant; that is, basal metabolism appears to represent the maintenance of a capacity to perform work (Brody, 1945; Kleiber, 1961; Dolnik, 1967; see other reviews in this volume). Whether developing birds, especially altricial nestlings, are capable of greater rates of work than similarly sized adults seems doubtful, however.

A large component of basal metabolism may represent heat produced

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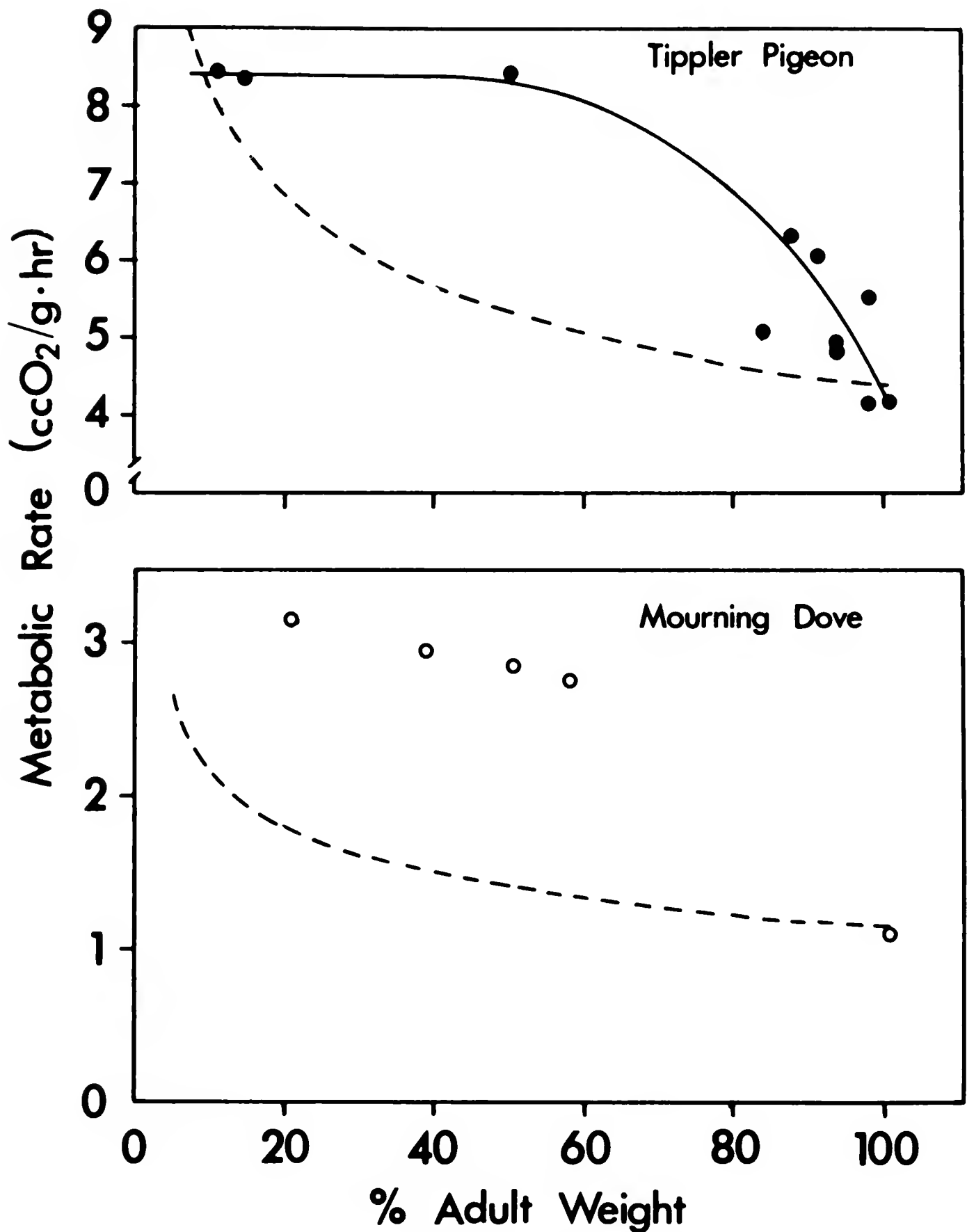


FIG. 20. Metabolic rates of nestlings of Tippler Pigeons at 30°C (Riddle, et al., 1932) and Mourning Doves at 39°C (Breithenbach and Baskett, 1967) as a function of proportion of adult weight (254 g and 126 g (Cheney and Cheney, 1967)). Metabolism of adult Mourning Doves at 30°C from Riddle, et al. (1932). Aschoff-Pohl (1970) predictions for resting, nonpasserine adults are indicated by dashed lines.

to maintain elevated body temperatures. If this were the case, body temperatures at ambient temperatures above lower critical temperature would be regulated by changes in insulation and evaporation, which can respond more quickly than metabolic heat production to changes in ambient temperature. It may be significant that the increase in basal metabolism of developing birds parallel the development of homeo-

TABLE 25
Calculation of the Maintenance Energy Expenditure of Growing White Leghorn Chickens from data of Medway and Kare (1957) on Metabolic Rate and Growth Rate (see text).

W	Metabolic rate ¹		Growth rate		Work of biosynthesis (kcal/day) ⁴	Maintenance energy expenditure	
	(cal/g·hr)	(kcal/day)	(g/day) ²	(kcal/day) ³		(kcal/day) ⁵	(cal/g·hr)
0.05	10.4	22.46	6.47	10.64	3.55	18.92	8.76
0.1	7.3	31.53	9.95	16.81	5.60	25.93	6.00
0.2	5.9	50.98	13.90	24.75	8.25	42.73	4.95
0.3	4.9	63.50	15.60	29.18	9.73	53.78	4.15
0.4	4.25	73.44	15.83	31.03	10.34	63.10	3.65
0.5	3.8	82.08	14.97	30.69	10.23	71.85	3.33
0.6	3.45	89.42	13.24	28.33	9.44	79.98	3.08
0.7	3.15	95.26	10.79	24.05	8.02	87.24	2.88
0.8	2.9	100.22	7.71	17.89	5.96	94.26	2.72
0.9	2.75	106.92	4.10	9.87	3.29	103.63	2.67
1.0	2.6	112.32	0.00	0.00	0.00	112.32	2.60

¹ Empirical values.
² Calculated from the Gompertz equation fit to observed growth data.
³ Growth rate times caloric equivalent of wet weight calculated from equation in Table 24.
⁴ Assuming a production efficiency of 75%, equal to 1/3 of the tissue accumulation.
⁵ Metabolic rate minus work of biosynthesis.

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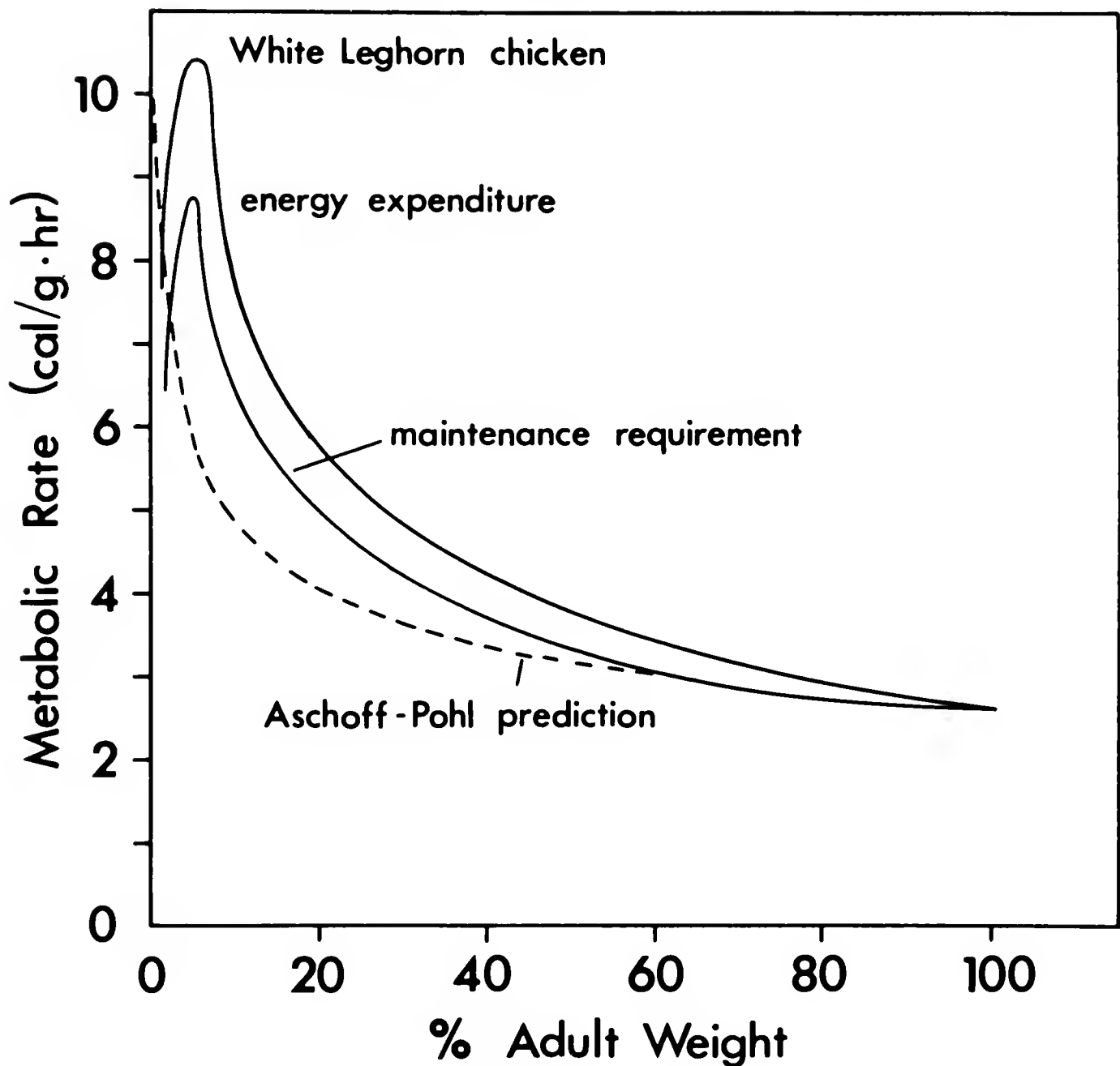


FIG. 21. Energy expenditure (basal metabolic rate), energy requirement of maintenance, and Aschoff-Pohl prediction of BMR for adults, as a function of body weight (adult weight 1,800 g) in female White Leghorn chickens (based on data in Medway and Kare, 1957, and Table 25).

thermic capacity. Furthermore, when metabolism of chicks exceeds the metabolic rate of comparably sized adults the young are growing feathers, and the blood-filled feather quills may be a major avenue of heat loss. The general notion that developing feather quills influences heat loss and metabolism has been discussed in passing by King and Farner (1961:247), Breitenbach and Baskett (1967), and Yarbrough (1970).

GROWTH RATE AND NESTLING ENERGETICS

Knowing the basal metabolism, growth rate, and energy content of tissues, we can estimate the total energy requirements of young birds during the development period (not including temperature regulation and activity). This, in turn, allows us to determine the amount of food that the precocial young must gather, or the altricial young must be fed, and to assess the influence of growth rate on the overall energy

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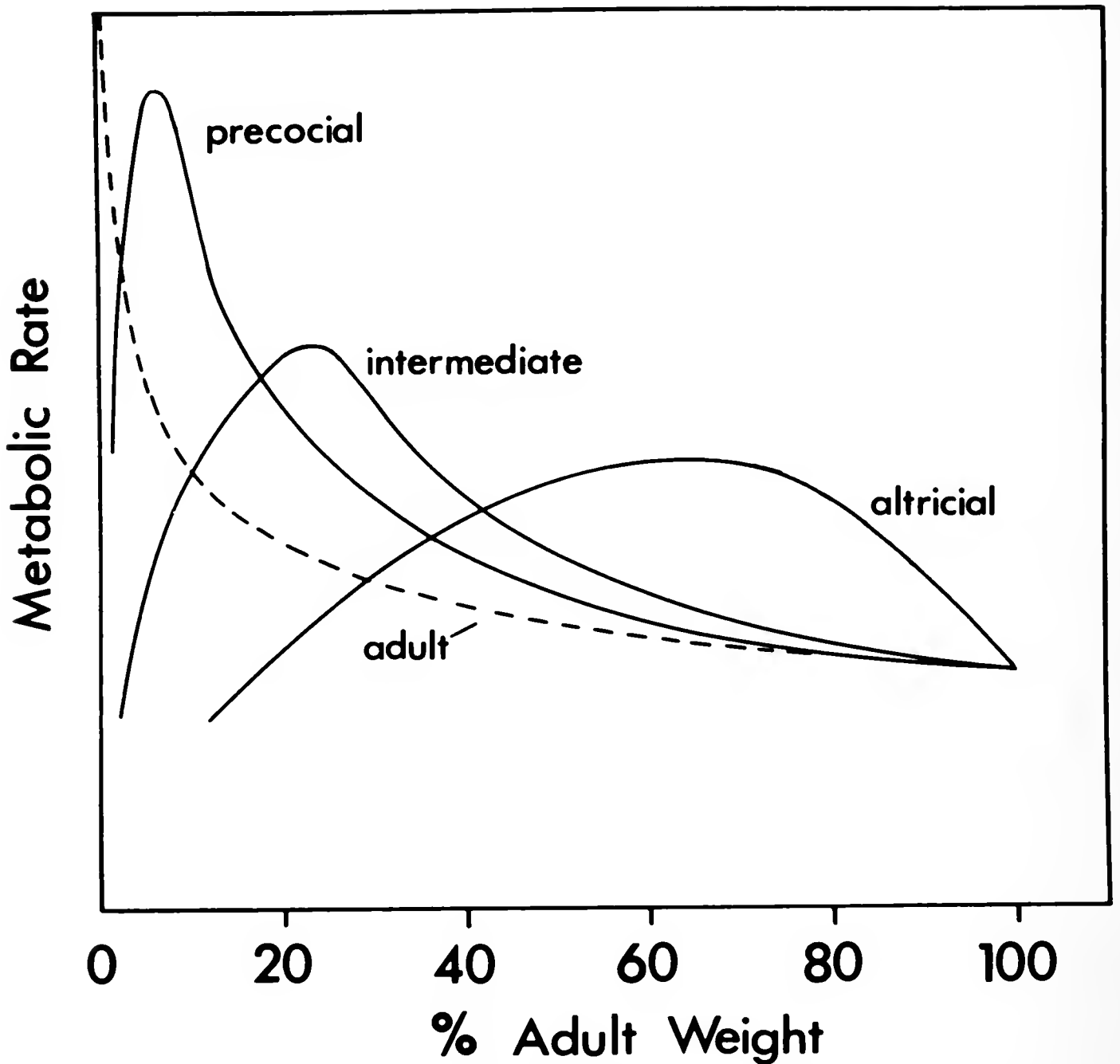


FIG. 22. Schematic diagram of basal metabolic rate as a function of body size for adults, precocial young, altricial young, and forms intermediate between precocial and altricial modes of development.

budget of the young. Energy requirements have been calculated from patterns of energy expenditure shown in Figures 15 through 20, energy equivalents of body weight presented in Table 24, growth equations presented in Ricklefs (1968, 1973a) or calculated here, and assuming an efficiency of production of 75%.

The total energy requirements of two self-feeding, precocial species, the White Leghorn chicken and the Dunlin, are shown in Figures 23 and 24. In both species, the maintenance energy requirement is always greater than the growth requirement, which is probably characteristic of self-feeding species. By the time Dunlin chicks have attained 30% of adult weight, and chickens about 50% of adult weight, their energy requirements approach nearly maximum rates and level off during the remainder of the growth period. At this time, the requirement for growth decreases just about as fast as the energy requirement for maintenance increases.

Until the total energy requirement of the young reaches a plateau,

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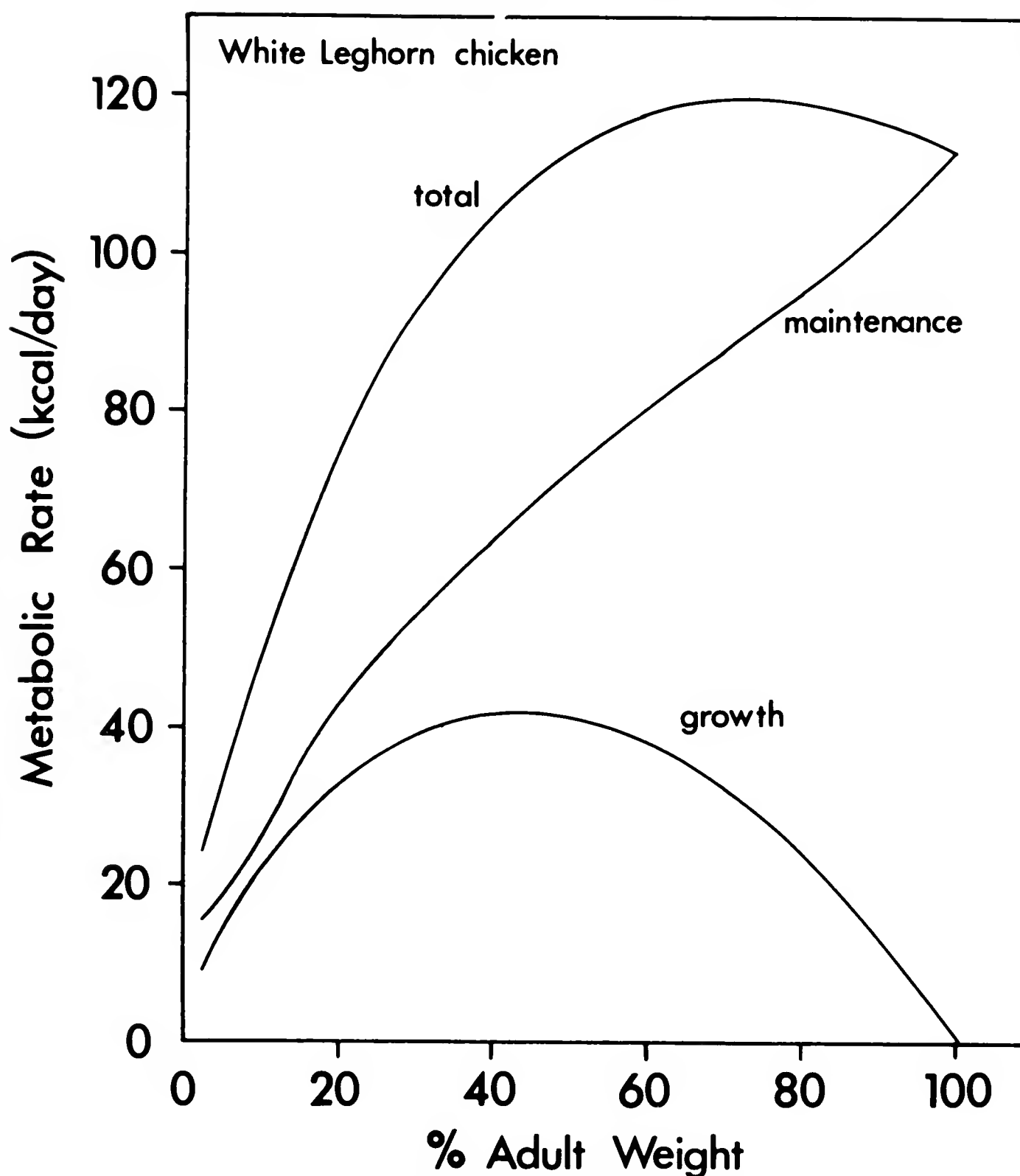


FIG. 23. Energy requirements of growth and maintenance in the White Leghorn Chicken (after data in Medway and Kare, 1957; see text). The total energy requirement is the sum of the maintenance and growth energy requirements.

the chicks must gather food for basic maintenance and growth faster, relative to their body weight, than they will have to later in the development period. Chicks that are only 30-50% of adult size must gather food as rapidly as fully grown birds. The early growth period is apparently the most critical energetic stage for the young; it is not surprising that precocial chicks hatch with large yolk reserves and that the young remain closely associated with their parents.

The total energy requirement of Sooty Tern chicks, which develop precocially (and grow as slowly as other precocial species (Ricklefs, 1972)) but are fed by their parents, is shown in Figure 25. This pattern differs from that of self-feeding precocious species in that the growth

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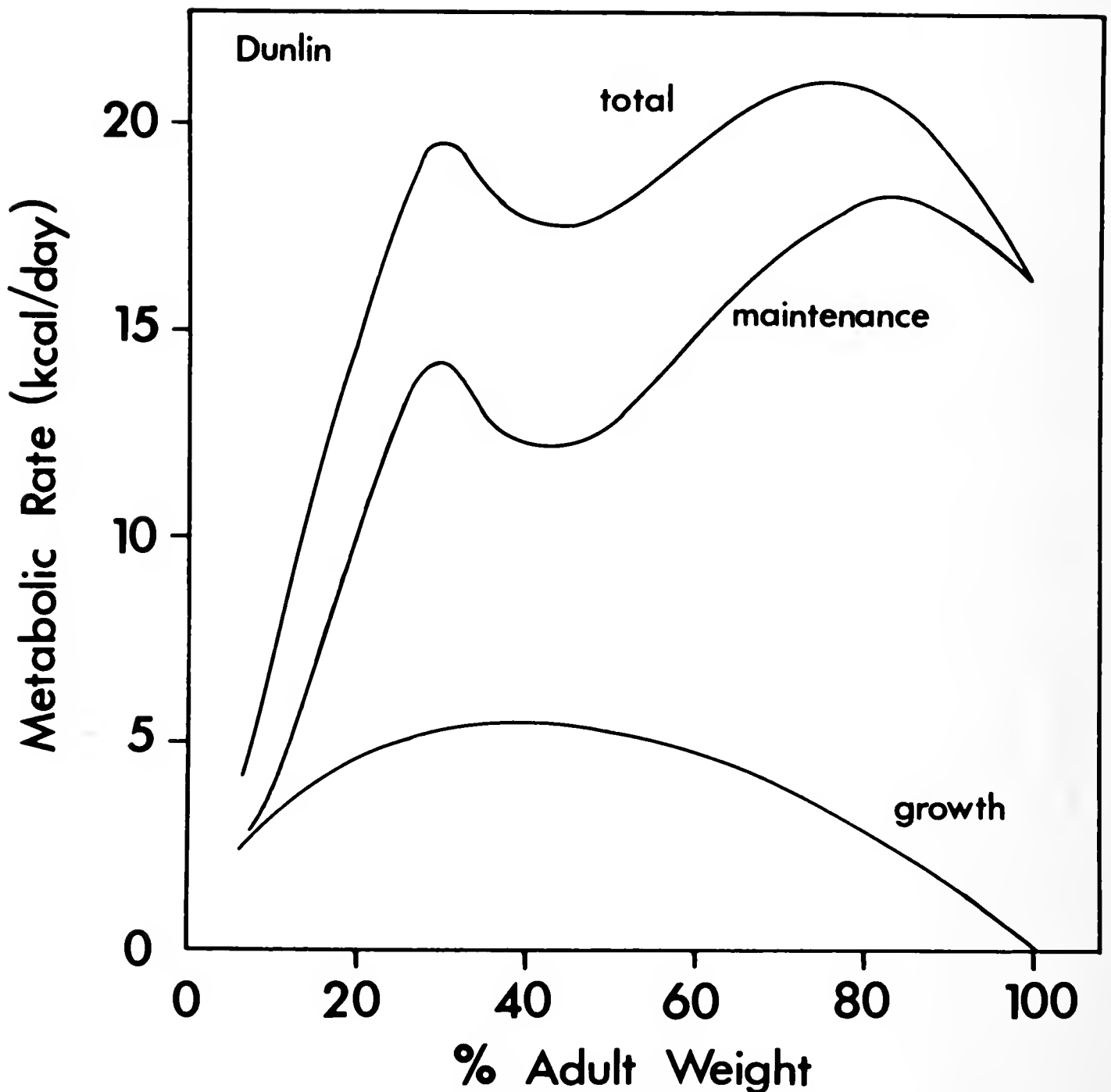


FIG. 24. Energy requirements of growth and maintenance in the Dunlin (after data in Norton, 1970; see text).

energy requirements of small young are greater than their maintenance energy requirements. As in the chicken and Dunlin, however, the total energy requirement of the Sooty Tern reaches a plateau when the young have attained about 40% of adult weight.

If the ability of adult Sooty Terns to gather food for their young does not change during the nestling period, chicks utilize the energy delivery capacity of the parents very efficiently. To raise young, adult terns must deliver a maximum of about 27 kcal/day; the requirements of the young hover around that level for most of the development period. In fact, growth to 40% of adult weight occurs within the first week or 10 days of the 50-60 day nestling period. The growth rate of the Sooty Tern is apparently set to maximize energetic efficiency. Increase in growth rate would increase the maximum combined growth and maintenance energy requirement of the young; decrease in growth rate would not reduce the maximum value of this combined energy requirement, but would merely delay its attainment.

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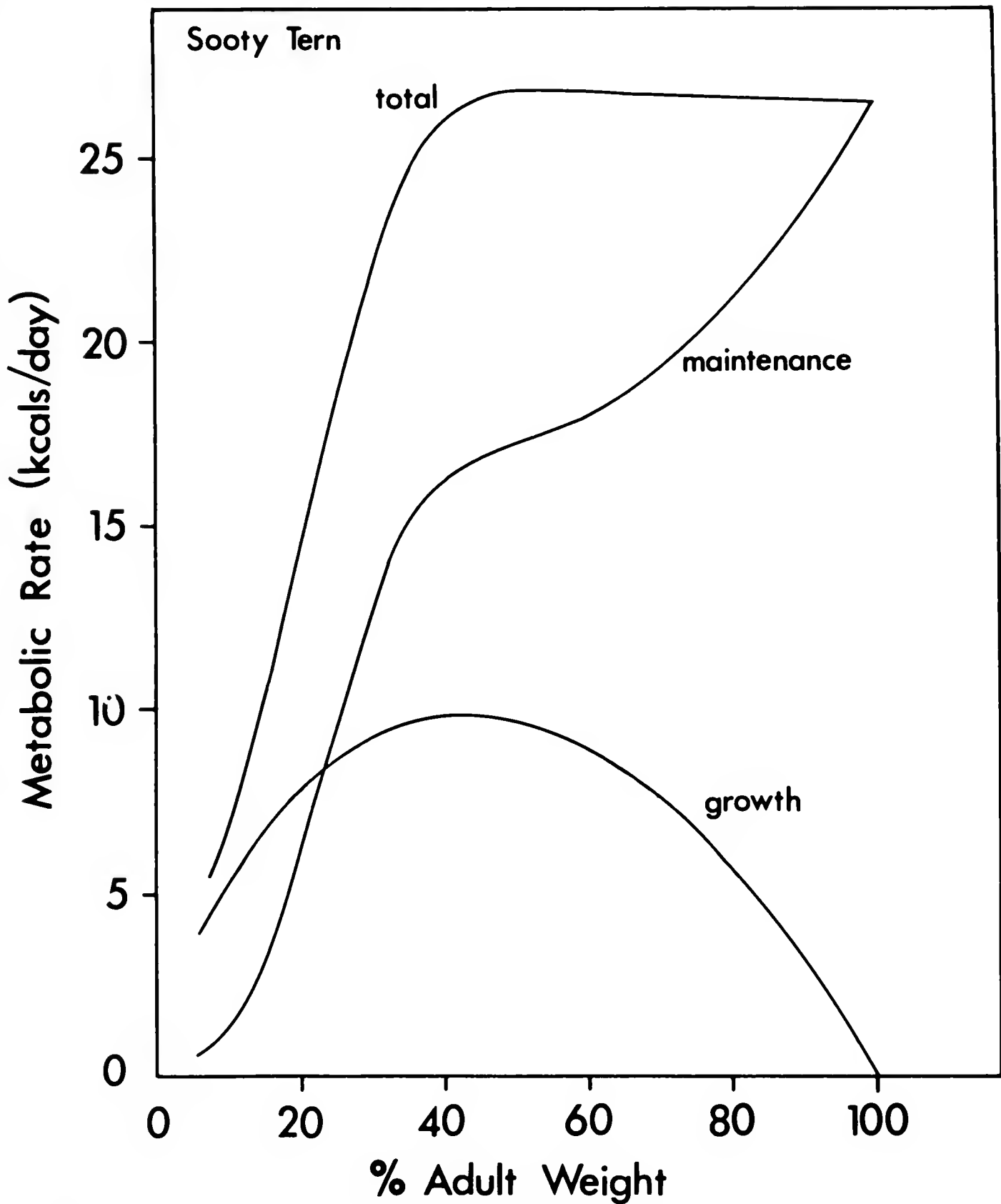


FIG. 25. Energy requirements of growth and maintenance in the Sooty Tern (after unpublished data of Ricklefs and White; see text).

Energy requirements for a hypothetical “sparrow” (Fig. 26) were calculated for a species with an adult body weight of 12 g, a growth curve fitted by a logistic equation with $K = 0.60$, metabolism ($\text{ccO}_2/\text{g}\cdot\text{hr}$) $= 2.6 + 2.7W$ (based on the Chipping Sparrow), and a biomass energy content of (kcal/g wet weight) $= 0.7 + 1.3W$ (based on the Rufous-winged Sparrow). In this rapidly growing sparrow, the energy requirement for growth exceeds the maintenance requirement until 70% of adult weight is attained. Also, the maximum total energy requirement is not reached until about 80% of adult weight is attained.

The energy expenditure of sparrows measured by oxygen consump-

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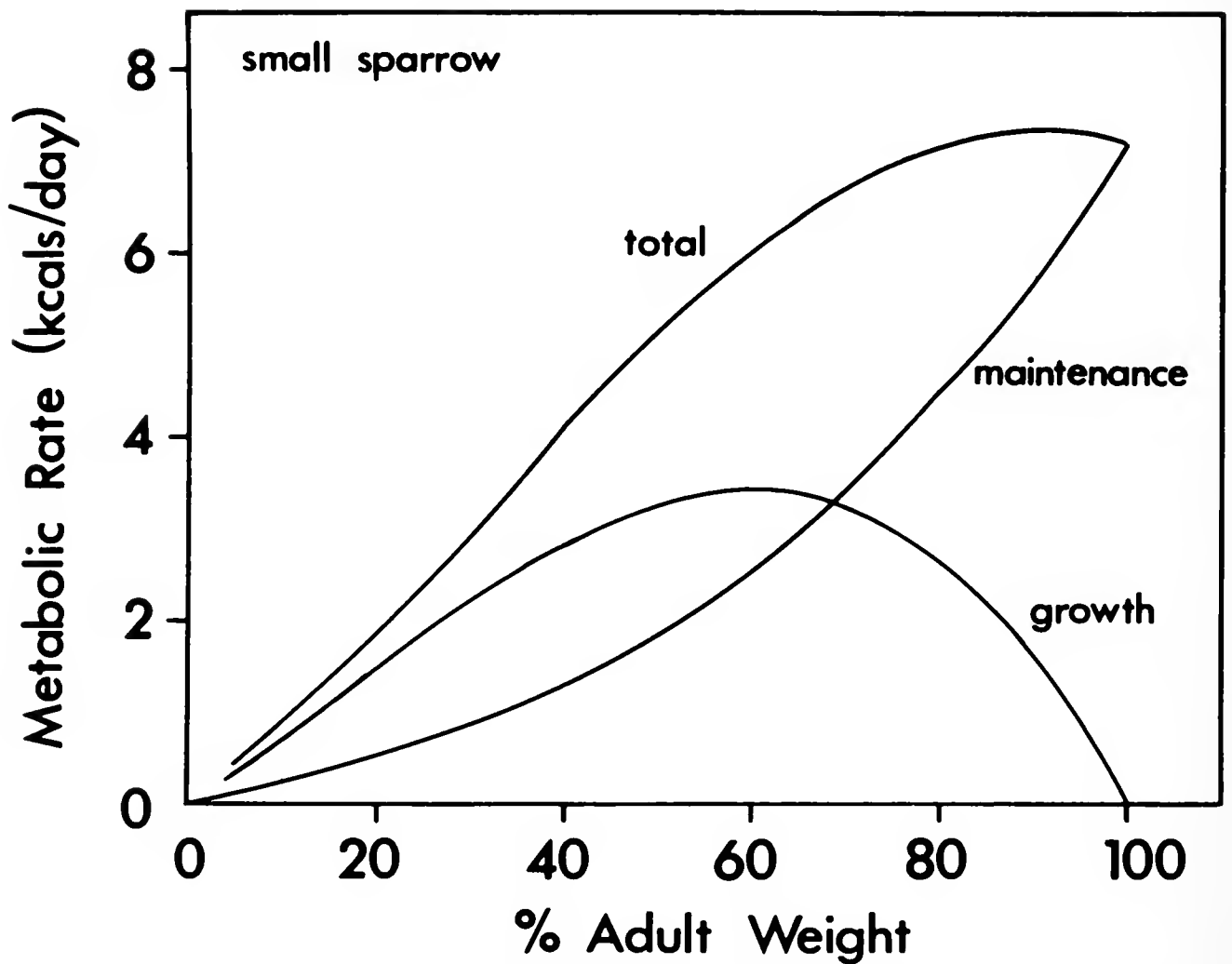


FIG. 26. Energy requirement of growth and maintenance in a hypothetical small Sparrow (see text).

tion increases to above adult levels during the nestling period. Oxygen consumption in Starlings appears to decrease to adult levels before the young leave the nest (Fig. 27). This decrease probably occurs in all species before the young are independent of parental feeding. I have, therefore, created another hypothetical passerine with $W = 70\text{g}$, K (logistic) = 0.40, energy content (kcal/g) = $0.7 + 1.1 W$, and energy expenditure based on the Starling data in Figure 27, minus 30% for SDA. Even though the growth rate of this hypothetical species is lower than that of the "sparrow" introduced above, high maintenance and growth requirements during the middle of the growth period combine to cause a definite peak in the total energy requirement at 60-80% of adult weight (Fig. 28). This pattern would not be changed substantially by incorporating SDA and energy expenditure for activity and temperature regulation. The hypothetical passerine differs from the Sooty Tern in that a change in growth rate would substantially alter the maximum daily energy requirement of the young.

The energy requirement models for the hypothetical starling-like bird and the hypothetical sparrow-like bird differ primarily because the per gram metabolic rate of the starling-like species decreases as growth is completed. In fact, metabolism has not been measured for nestling sparrows much heavier than 70-80% adult weight because the young fledge well before body weight growth is completed. The metabolic rate of the Starling does not begin to decrease until this point. The

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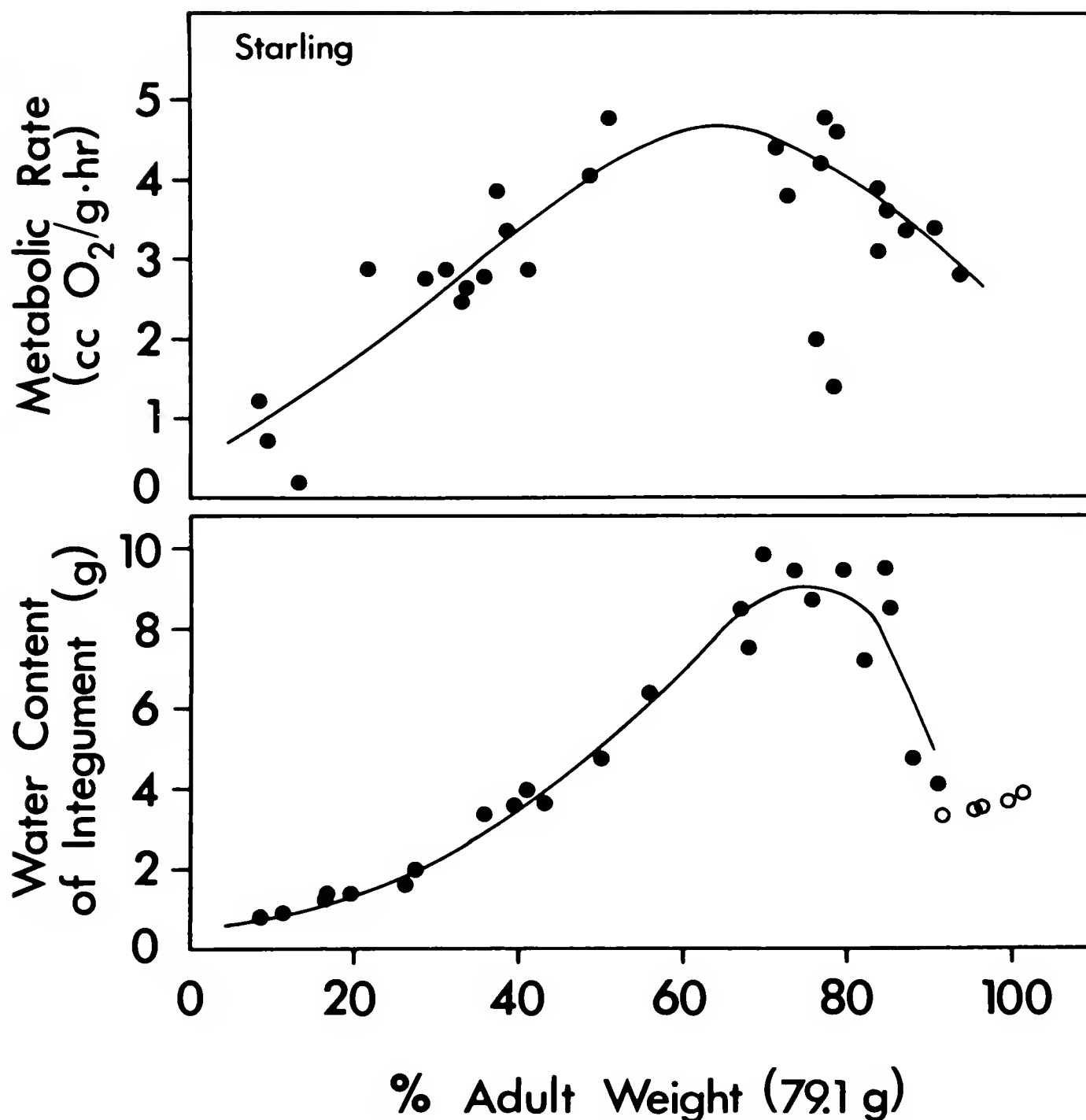


FIG. 27. Above: Oxygen consumption of Starling nestlings, replete and at 33-37°C, as a function of percent of adult weight (79.1 g) attained (Ricklefs unpublished data). The Aschoff-Pohl prediction for a resting passerine is 2.03 ccO₂/g·hr.

Below: Water content of the integument (skin and feathers) of the Starling as an index of the heat loss potential from blood in developing feather quills (Ricklefs, unpubl.).

energy model of the starling-like bird is probably the more representative pattern for altricial species, although the form of the energy expenditure curve with respect to body weight must be influenced by the degree of precocity of the young (for example, by the development of plumage in relation to the growth curve for body weight). Furthermore, because developmental changes continue to occur after the young have reached adult body weight, one might also expect further changes in maintenance metabolism.

By estimating maintenance energy requirements from the metabolism of birds under standard conditions in the zone of thermoneutrality, one overestimates the contribution of growth energy requirements to the total energy budget. The energy requirements of

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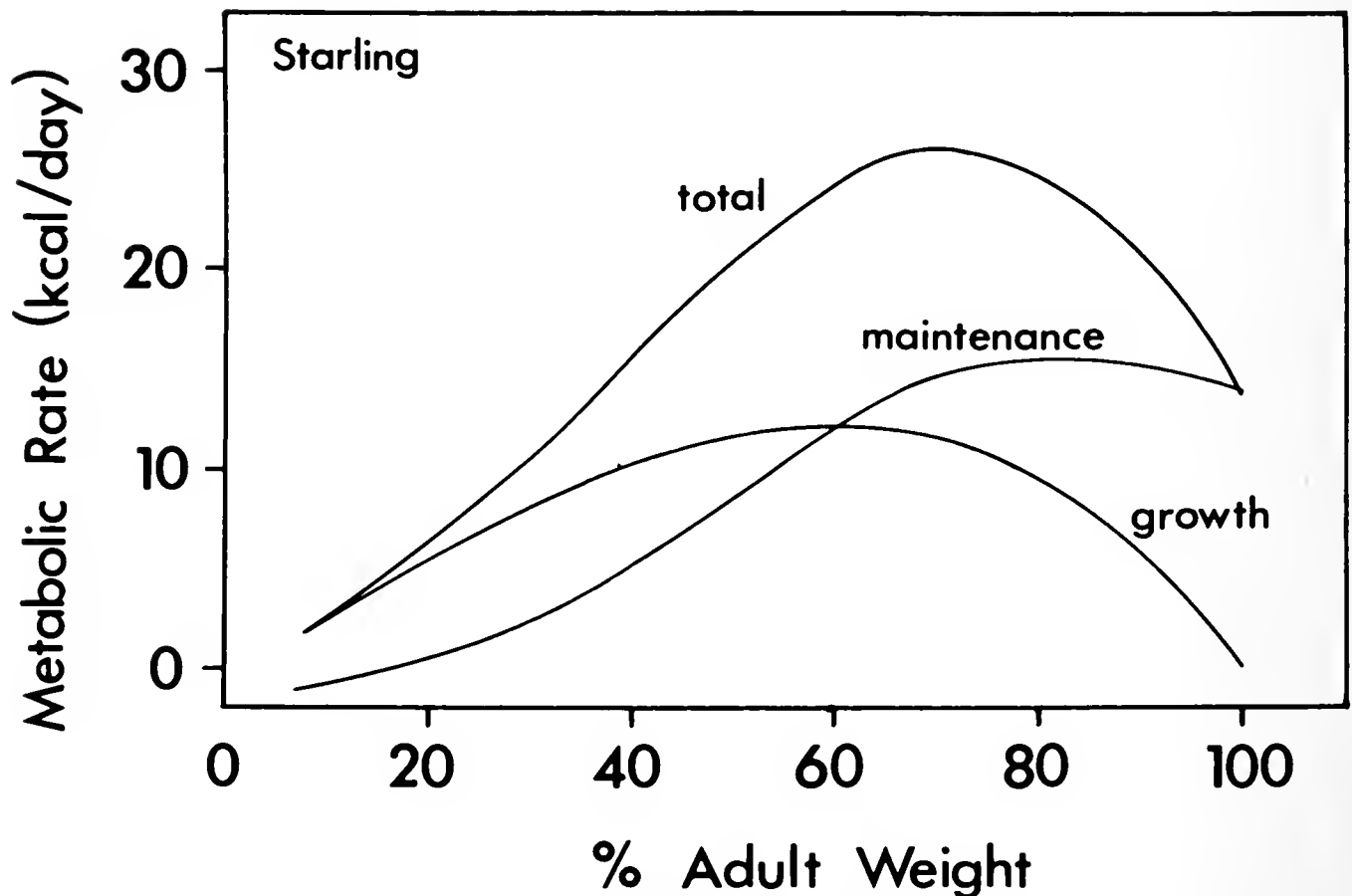


FIG. 28. Energy requirements of growth and maintenance for a hypothetical bird based on the Starling (see text for assumptions).

thermoregulation and activity are difficult to measure directly for birds under natural conditions but they can be estimated indirectly as the difference between metabolizable energy intake and measured energy requirements for growth and maintenance under standard conditions. Dunn (1973) has summarized estimates of energy requirements for activity and thermoregulation from studies on four species (Table 26). Estimated costs of thermoregulation range between 10 and 60% of the thermoneutral maintenance requirement (TMR) and costs of activity range between 30 and 100% TMR. Sums of these costs for each species range between 40 and 150% TMR. However tentative these estimates may be, they emphasize the importance of expanding the laboratory approach to growth physiology to include the energy requirements of birds in their natural environments.

FAT STORAGE AND WEIGHT RECESSION IN NESTLINGS

The young of many species weigh considerably more than adults during the development period and often lose much of this excess weight before fledging. Deposition and subsequent utilization of fat by the nestling has been suggested as the cause for this pattern of weight change. Birds are thought to require the additional energy provided by fat reserves either because of increased energy demand caused by rapid feather growth or because adults abandon the young at the end of the nestling period. Lack (1968a) suggested additionally that fat deposits in swifts and many offshore-feeding seabirds (in which fat deposits are best developed) act as insurance against erratic feeding conditions. He cited the frequent decline in weight to adult level be-

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TABLE 26

Costs of Activity and Thermoregulation in Nestling Birds After the Age at which Brooding Ceases (from Dunn, 1973).

Species ²	Ambient temperature (°C)	Energetic cost ¹ of:		Sum
		Thermo- regulation	Activity	
Double-crested				
Cormorant	15-25	60	75	135
Herring Gull	15-25	15	80	95
Dunlin	5	50 ³	100	150
Starling	12 ⁴	10	30	40

- ¹Expressed as a percentage of the thermoneutral maintenance requirement obtained from measurements of oxygen consumption of fed birds.
- ²Data from Dunn (1973), Dunn and Brisbin (unpubl.), Norton (1970), and Westerterp (1974), respectively.
- ³No allowance made for brooding, absorbtion of solar radiation, or nighttime hypothermia.
- ⁴Ambient temperature outside nest box.

fore fledging as an indication that fat stores are not needed by the young after fledging. On the other hand, parental care generally does not extend beyond the fledging period in species that fledge considerably above adult weight, presumably with large deposits of stored fat.

Richdale (1954) demonstrated that the weight loss of albatrosses, and probably other Procellariiformes, at the end of the nestling period is not due to starvation, but a starvation period of a couple of weeks is apparently characteristic of many shearwaters. Lack (1968) suggested that the starvation period in these species enabled adults to begin their migrations early.

The young of many species become quite fat during the nestling period. For example, Nelson (1966) reported that young Gannets (*Sula bassana*) leave their nesting colonies with up to 1,000 g of fat deposits (adult weight about 3,200 g). Nestling Leach's Petrels (adult weight about 40 g) have been collected with more than 30 g of fat (Ricklefs, Cullen, and White, unpubl.)

Patterns of fat storage are partly obscured by the fact that the water content of the body usually exceeds adult levels in nestlings and decreases with the maturation and drying out of the feathers. Nestling Barn Swallows (*Hirundo rustica*) exceed adult weight by about 15% on the 12th day of the nestling period and weigh slightly less than adults

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by the time they fledge at 20 days (Stoner, 1935). The fat content of the young increases slowly to fledging and rarely exceeds 2 g. The excess of nestling weight over adult weight and the decline in nestling weight before fledging can be accounted for entirely by changes in water content, primarily of the integument (Ricklefs, 1968a). The quills of developing feathers consists primarily of water (Ricklefs, 1967; Lillie, 1940), but as the feather grows and matures, its water content decreases considerably.

Fat dominates the composition of Leach's Petrel nestlings, but changes in water content also play an important role in weight changes. In a series of nestlings aged 1 to 63 days (about to fledge), fat content increased throughout the entire nestling period while at about 40 days water content peaked at about 0-10 grams above adult levels (Ricklefs, Cullen, and White, unpubl.). We did not obtain enough birds during the last 10 days of nest life to determine the cause of rapid weight loss at this time. An analysis of body components indicates, however, that the decline of body weight to adult levels from the nestling peak must result from loss of fat. At 50 days nestling petrels carry about 20 g of fat which, at a metabolic rate of about 20 kcal/day, is sufficient reserve for nine days without food. The significance and eventual fate of energy reserves in petrels, and in other species that apparently utilize their reserves before fledging, are poorly known. That stored fat may function as insulation has not been explored, however. The prevalence of fat storage among species at high latitudes, and the location of 70-80% of the fat in Leach's Petrel nestlings in subcutaneous deposits, suggests that this material could provide insulation.

STARVATION AND HYPOTHERMIA IN YOUNG BIRDS

Ability to survive long periods without food is an important requirement of nestlings of species whose food supplies are erratic. Indeed, Lack (1968a) argued that the fat stores of nestling swifts and petrels, among others, provide just this sort of energetic insurance. These species feed at great distances from their nests on extremely ephemeral food supplies: small aerial insects or marine surface invertebrates. The ability of birds to exploit these resources can be reduced for long periods by unfavorable weather (see Lack and Lack, 1951; Lack, 1956).

For a given level of energy reserves, survival time without food can be increased by reducing metabolism; for example, by shutting down growth processes and reducing body temperature. Periodic reversible hypothermia is well known in adult hummingbirds (Hainsworth and Wolf, 1970) and in caprimulgiforms and swifts (Bartholomew, et al., 1957). West and Norton (MS) have noted that calidridine sandpiper chicks regularly allow body temperature to drop 10°C below adult levels, until the chicks are old enough to fly, without any apparent reduction in activity. This strategy of partial hypothermia undoubtedly reduces the heat loss of these small, poorly insulated young (see Fig. 12).

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Survival times of nestling birds are well correlated with fat reserves. Of eight Leach's Petrels maintained without food for a week, only one, the youngest, died after 6 days (Ricklefs, Cullen, and White, unpubl.). The other nestlings had lost 30-40% of their original weight by the end of the experiment. In similar starvation experiments, Sooty Terns lost 30-40% of their initial weight in 3-4 days and could not survive much longer. Most passerine nestlings do not survive more than 2-4 days without food.

Baldwin and Kendeigh (1932) maintained nestling House Wrens without food at temperatures of 37°C and 19°C. At the higher temperature survival time increased from about 10 hours at hatching to 50 hours at 15 days. Before dying at 37°C, a 2-hour old and a 2-day old bird lost 14-15%, and an 11-day old nestling lost 43% of initial weight. Older nestlings evidently have greater food reserves relative to metabolic rate. However, at 37°C dehydration rather than starvation may have caused death. At 19°C survival time decreased from about 35 hours at hatching to 17 hours at 7-11 days and then increased to 25 hours at 15 days. Because metabolic requirements at low temperature do not change as a function of age after 10 days (See Kendeigh, 1939) the increase in survival time after the onset of thermoregulation must be related to increasing energy stores. Survival time of nestlings younger than 7 days of age must be related to their tolerance of low body temperatures, because a 2-day old and a 4-day old nestling lost only 0.7% and 1.4% of their body weight, respectively, before dying at 19°C.

In my experience, nestlings of passerine species old enough to regulate their body temperatures do not become hypothermic until they are on the verge of death (see Gotie and Kroll, 1973, for a possible exception). Koskimies (1948) also found this to be true of nestling Swifts (*Apus apus*) (4-5 weeks old). Four young fasted at 24°C and survived an average of 230 hours (range 205-290), whereas four adults survived only 110 hours (range 100-135) under the same conditions. The young weighed more than the adults at the beginning of the fast and lost more weight before death, presumably owing to greater reserves of fat:

	Weight (g)			% Initial
	Initial	At death	Loss	
Adults	42.2	26.1	16.1	38
Nestlings	49.2	23.2	26.0	53

Body temperatures of the nestling swifts fluctuated within the normal range (38-40°C) during the first few days of the fast. But after day 6 body temperatures dropped to a few degrees above ambient temperature at night; the degree and duration of hypothermia in-

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creased daily until death. During daylight hours, temperatures returned to normal, but for a shorter period each day. Adults began to exhibit nocturnal hypothermia on day 4, the day before most of them died, but normal body temperature was recovered during the daytime on the day of death. Hypothermia in the Swift appears to be a pathological expression of starvation, but its reversibility during the day suggests that it may confer survival value under extreme conditions.

We have found a similar situation in Leach's Petrel (Ricklefs, Culen, and White, unpubl.). Normal body temperatures and wing length growth were maintained under fasting conditions until birds were on the verge of death. When hypothermia did occur, it was clearly reversible and body temperature appeared to be regulated somewhat above ambient temperature rather than conforming completely to the temperatures of the surrounding air.

Hypothermia actually seems a poor strategy of coping with unpredictable food shortages. Lowered body temperature reduces metabolism (Koskimies, 1948), but also slows growth and extends the development period, thereby exposing the young to increased risks of predation, erratic food shortages, and seasonally poor feeding conditions. Where fat storage is available as a strategy of development, it will always be a superior alternative to hypothermia. The latter must be reserved as a last-ditch attempt to extend survival time.

ENERGETIC INDEPENDENCE OF THE YOUNG

The age at which young birds begin to feed themselves, thereby releasing adults to initiate additional breeding attempts or to engage in molt or migration, varies considerably among species. Precocial young feed themselves from hatching with varying degrees of assistance from their parents. Megapode chicks are completely independent; gallinaceous chicks are brooded and shown food by their parents; loons, grebes, and rails are fed by their parents for a brief period after they hatch (Nice, 1962). Early acquisition of energetic independence by precocial chicks is related to their mode of development. Differences in the degree of independent feeding among precocial species could probably be related to subtle differences in development, as well as to the character of their food supply. But we have too little information on the ecology and early development of precocial young to determine the factors that influence the choice of development strategy.

Species with precocial young use food resources that do not require flight to be procured. Thus the precocial mode of development appears to be limited to ground feeding terrestrial species (e.g., galliforms and many charadriiforms), and to inshore feeding aquatic birds (e.g., ducks and some murrelets). Birds that are specialized to feed on prey that must be searched for, or pursued, by flight or even by rapid movement on the ground, usually exhibit altricial development. Young of such species do not acquire energetic independence until they are fully

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grown and nearly as agile as adults. But even among altricial species the timing of energetic independence varies considerably.

Few quantitative data have been obtained on parental feeding of young altricial birds after they have left the nest, so our estimates of the duration of the dependency period are based largely on anecdotal observations. The young of most temperate passerines are totally self-feeding when they are 25 to 30 days old and are usually completely independent after 30 to 45 days (Ricklefs, unpubl.). For example, Morton, et al. (1972) observed feeding rates of newly fledged White-crowned Sparrows near Tioga Pass in the Sierra Nevada Mountains of California. The nestling period is 9-10 days and broods are fed 12-16 times per hour during the last five days of the nestling period. Parents were observed to feed fledged broods at comparable rates on days 10, 13, and 14, but less than five times per hour on days 11, 15, and 17 (2-5 hours observation each). Between days 10 and 15 the young sparrows spent most of their time perched in bushes near the nest, and were poor fliers. The young began to forage for themselves between 16 and 20 days of age, even though they were fed occasionally until three to four weeks old. In three cases eggs of a following brood were laid when the young of the first brood were 16, 17, and 18 days old.

Morehouse and Brewer (1968) observed a similar pattern in the Eastern Kingbird (*Tyrannus tyrannus*). Young were fed entirely by the adults for 30-35 days after hatching. Parental feedings thereafter occupied a minor role in the energetics of the young, which were nonetheless fed occasionally to 50 days of age. Most aspects of development, including growth, fledging, self-feeding, and independence, require about 50% longer in the Kingbird than in the White-crowned Sparrow. Observations on a brood of Mangrove Swallows (*Tachycineta albilinea*) in Panama indicated that energetic independence is acquired between 30 and 40 days after hatching (Table 27), although young do not leave the nest area until 40-50 days of age (unpublished observations). Tropical species feed their young, at least to some extent, for much longer periods (up to 50-60 days of age) than temperate species (Fry 1967; Ricklefs, 1969a; Fogden, 1972).

Patterns of attaining energetic independence in seabirds are quite diverse. Many species are wholly independent at fledging, whereas others are fed by the parents for many months after fledging, although it is not generally known how much of the energy intake is provided by the adults or to what degree parental feeding serves a necessary energetic function. Perhaps parental feeding can serve the same purpose as courtship feeding and feeding the incubating female on the nest often do, namely to maintain behavioral bonds between individuals.

In the family Sulidae (boobies and gannets), tropical species have small clutches, long periods of development, and care for their young for two to three months after fledging (Lack, 1968a; Nelson, 1970). The cold-water gannets have more rapid development and they are

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TABLE 27

Activity of a Pair of Adult Mangrove Swallows and Their Single Fledged Young on Barro Colorado Island, March 1968 (Ricklefs, unpubl.).

Date	Time	Age of fledgling (days from hatching)	Feedings per hour	Percent time spent flying	
				Adults	Fledgling
March 3	1651-1730	27	9	51 ¹ , 97 ²	0
4	0639-0656	28	18	71 ³	12
4	1400-1438	28	8	76	2
7	1659-1759	31	36	81	13
8	1255-1355	32	6	58	5
11	1700-1745	35	0	98	20
12	0935-1015	36	3	89	67
15	1656-1726	39	0	100	80

¹Adult did not feed young.

²Adult fed young.

³Both adults feeding young; data combined.

completely independent at fledging. The independence of young gannets is undoubtedly facilitated by the fledgling's leaving the nest with substantial reserves of fat. Patterns of parental care in seabirds apparently parallel latitudinal trends in passerines.

Two general hypotheses have been proposed to explain differences in the timing of energetic independence. The most frequent argument is that the complete acquisition of self-feeding is delayed when foraging requires special skills that can be perfected only through experience, or when the food supply is so sparse (as indicated by small broods) that young have difficulty finding sufficient food for themselves until their feeding skills are well developed (Ashmole and Tovar, 1968). Feeding skills undoubtedly do improve with age and experience (see, for example, Orians, 1969; Dunn, 1972; Recher and Recher, 1969).

A second argument, based on demographic considerations, relates the extension of parental care after fledging to the relative value of the young, measured in terms of how easily they may be replaced (Ricklefs, 1969a). Where clutch size and nest success are low, fledged young represent the equivalent of many more eggs laid than where clutches are larger and nests are more successful. According to this reasoning, which is not incompatible with the argument outlined above, parental care should be longer in tropical species than in temperate species.

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Therefore, field observations are compatible with both hypotheses and do not permit us to distinguish between them without acquiring more data. It is unfortunate that this aspect of reproductive biology has been so neglected by field ornithologists.

ENERGETICS OF ADULT FORAGING

The amount of food that parents can deliver to their young depends on the availability of food and on the intensity of their foraging effort, which affects both feeding rate and adult energy expenditure. The former is completely outside the scope of this review, but knowledge of energetic expenditures for foraging is crucial to understanding how energetic considerations determine brood size in altricial species.

If adults are to forage at all, whether for themselves or for their young, they must gather energy at a greater rate than they use it in foraging. Beyond that point the duration and intensity of foraging effort are limited by other maintenance needs of adults, such as preening, territorial defense, and predator detection, and by physiological limits to the rate of energy expenditure, either through limits to energy mobilization, work potential of muscles, or ability to dissipate heat.

Unfortunately, the energetics of foraging activity in free-living birds are difficult to measure. Two techniques are available: direct measurement of energy expenditure by turnover rates of doubly-labelled water (D_2O^{18}), and indirect estimation of energy budgets by measuring time budgets and estimating or measuring energetic equivalents of various activities. The D_2O^{18} method is expensive and is limited to the measurement of average energy expenditure over periods of a day or more, depending on the relative metabolic rate of the subject (McClintock and Lifson, 1958; LeFebvre, 1964; Lifson and McClintock, 1966; Utter and LeFebvre, 1970, 1973; see, also, King in this volume). Time budgets, on the other hand, are laborious and their energetic equivalents are based on estimates of varying quality. Because of these methodological limitations, progress on the relationship between adult metabolism and reproduction will be very slow. But a few studies demonstrate the types of information that can be obtained.

The only direct measurement of energy expenditure during the breeding season involved use of the D_2O^{18} method for study of Purple Martins (*Progne subis*) (Utter and LeFebvre, 1973). Time budget data were simultaneously obtained, but unfortunately no indication is provided of how many young were being fed or how old they were. Metabolism was measured on two males and two females, but only the females fed young frequently. Daily energy expenditure of the females was 28% greater than that of the males; the time spent in flight by males and females at the colony was 47% and 67%, respectively (Table 28). Energy expenditure calculated from the time budget corresponded closely to the direct determination, but this is not surprising since flight is the major component of the Purple Martin's energy

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TABLE 28

Time and Energy Budgets of Purple Martins During the Breeding Season (based in part on data in Utter and LeFebvre, 1973).¹

	Male	Female
Percent of day spent flying ²	47	67
Nest visits/bird · day	7	52
Energy equivalent of time budget (kcal/day):		
night (9 hrs at 0.54 kcal/hr) ³	4.83	4.83
day perched (0.81 kcal/hr) ⁴	6.44	4.01
day flying (3.5 kcal/hr) ⁵	24.68	35.18
total (kcal/day)	35.95	44.02
Direct measurement of energy expenditure by D ₂ O ¹⁸ method on four birds (kcal/day) ⁶	31.4, 36.9	40.6, 46.9

¹ Energetic equivalents of time budgets in this table differ slightly from Utter and LeFebvre's values because I used 49.2 g for the weight for adults of both sexes.

² Of 15 hours.

³ Calculated from appropriate equation of Aschoff and Pohl (1970) for BMR.

⁴ 1.5 x BMR.

⁵ Determined directly by Utter and LeFebvre (1970).

⁶ Assuming a respiratory quotient of 0.8 (see Utter and LeFebvre, 1973).

budget and Utter and LeFebvre (1970) had determined the energetic equivalent of flight directly. While foraging female martins used energy as rapidly as 700% BMR. Average energy expenditure of the adult females was about 340% BMR. If females flew 100% of the daylight hours, their daily energy expenditure would have been 57.33 kcal/day or 442% BMR.

Gathering food for nestlings is known to require a major portion of the time budget in many species. Male long-billed Marsh Wrens spend 80-100% of the daylight hours foraging during the nestling period (Verner, 1965). Allocation of time to singing, resting, preening, courtship, and nest construction is correspondingly reduced. Female Great Tits increase the length of their working day as the nestling period progresses and the young require more food (Kluijver, 1950).

Intensity of foraging may be limited below the maximum potential level by the ability of birds to dissipate heat. For example, when air temperature exceeds 35°C, Cactus Wrens (*Campylorhynchus brunneicapillus*) reduce the rate of feeding visits to the nest (Ricklefs and Hainsworth, 1968a). Wrens evidently cannot afford to lose the amount of water necessary for evaporative cooling at maximum foraging rates.

Heat dissipation apparently limits the time that Mangrove Swallows can spend foraging (Ricklefs, 1971). The swallows receive a substantial radiational heat load from the sun because they feed close to the sur-

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face of the water. Evaporative cooling is hindered by the high humidity of the tropical habitat. Even with young starving in the nest, swallows do not forage more than about 50% of the midday period, although they fly 80-95% of the cooler morning and evening hours. We can calculate an approximate energy budget for the Mangrove Swallow from Utter and LeFebvre's (1973) study of Purple Martins. We shall assume that night metabolism (11 hours) = 100% BMR, that daylight resting metabolism = 200% BMR, and that flight (65.3% of 13 daylight hours) requires 700% BMR. Total daily energy expenditure would be 331% BMR. To support a brood of four young with a maximum total energy requirement of 600% BMR (300% per adult), the adults would have to gather 631% BMR in 63.5% of daylight hours, or 34.4% of the day. This suggests that Mangrove Swallows can gather a maximum of about 1800% BMR per hour of flight while expending 700% BMR to forage. During at least some seasons adults can raise only one young (with requirement 150%) with similar foraging effort. In this case total daily energy requirement would be 406% BMR ($331 + 1/2 \cdot 150$), and the food capture rate while foraging would be 1180% BMR. If the capture rate dropped much below that level reproduction could not take place.

Birds that do not fly continuously while foraging may have quite different energy budgets while feeding young. Observations on a pair of Tropical Kingbirds (*Tyrannus melancholicus*) on Barro Colorado Island demonstrate this point (Ricklefs, 1971). The adults were observed foraging (sallying for flying insects) for eight hours over a three-day period when the two young were about half grown, and required food at an estimated daily rate of 100% adult BMR each. A total of 322 feeding sallies were observed. The young were fed after 63 (19.6%) of the sallies. If we assume that the adults ate the rest of the insects caught and that these prey had the same food value as those fed the young, each adult would have gathered 510% BMR per day ($1/0.196$), of which it would have consumed 410%. If the adults used energy at the rate of 100% BMR during a 12-hour night, 360% of the 24-hour BMR would have been expended during the daylight hours at a rate of 720% BMR. This value is surprisingly close to our estimate of the energetic cost of foraging in the Mangrove Swallow, even though Kingbirds apparently obtain a smaller return for their foraging effort. These calculations should not be taken too seriously, but they indicate the kinds of analyses that are possible, given the right system and careful observation (see, also, Koelink, 1972; Spaans, 1972).

WEIGHT CHANGES IN ADULTS DURING REPRODUCTION

Because reproductive activities require expenditure of energy, breeding could place a physiological strain on adults that might result in weight loss. In fact, decrease in adult body weight characterizes reproduction in many species, to the extent that several authors have equated weight loss to energetic strain of reproduction. For example,

Richdale (1947:166) stated, "This [greater weight in molting birds in February than in breeding birds in December] suggested that the month at sea during which the molt commences is a period of recovery from the stress of feeding young." Nice (1937:27) stated, "Feeding the young [Song Sparrows], on the other hand, is a strenuous period as is shown by the drop in weight." Finally, Newton (1966:93) suggested, "Such a pronounced fall in weight during the nestling period suggests that the act of feeding dependent young might place a considerable strain on parent Bullfinches."

Most species of temperate land birds weigh less in summer than in winter owing to plumage wear and a decrease in fat reserves, but one must associate weight loss with the reproductive cycle to demonstrate reproductive strain. Weight changes in females are complicated by changes in the size of the ovary and oviduct during the reproductive cycle. On the other hand, male Song Sparrows (*Melospiza melodia*) that were feeding young during the months of May and June weighed about 10% less than males not feeding young (Nice, 1937). Male Tree Sparrows lose 10-20% of their weight while feeding young; this loss is quickly recuperated after the young become independent (Heydweiller, 1935). Weights of male Bullfinches (*Pyrrhula pyrrhula*) were 6% lower when feeding young than during the incubation period (Newton, 1966). Female Blue Grouse (*Dendragapus obscurus*) lose almost 20% of their body weight during the incubation period and weights remain low while the young are brooded; body weights of hens captured without broods during the same time of year are at prebreeding levels (Redfield, 1973). Johnson and West (1973) have documented the loss of fat by Adelie Penguins (*Pygoscelis adeliae*) during the incubation period. Yellow-eyed Penguins (*Megadyptes antipodes*), however, gain weight during the incubation period, but lose weight slowly while feeding young. Broadbilled Prions (*Pachyptila vittata*) are as heavy at the end of the chick feeding stage as they are at the beginning of the reproductive period (Richdale, 1947). Adult Diving Petrels (*Pelecanoides urinatrix*) lose weight before the beginning of the incubation period, but body weight does not appear to change subsequently during the nesting cycle (Thoresen, 1969). Hussell (1972) has provided a nice demonstration of the effect of reproductive effort on body weights of Snow Buntings (*Plectrophenax nivalis*) by manipulating brood size. Females that fed broods of seven (normal brood size is five) were 8% lighter at the end of the nestling period than females which raised broods of four. Weights of males were not significantly affected by the increased brood size. Fisher (1967) showed that juvenile (nonbreeding) Laysan Albatrosses (*Diomedea immutabilis*) lose weight during the season of chick feeding to about the same extent as breeding adults. Other examples could be provided, but the observations are difficult to interpret for we do not know the extent to which changes in organs or constituents cause the weight change or the extent to which weight change alters adult survivorship.

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Adult Ringed Doves gain about 6-8% of adult weight during the incubation period and then lose all of that increase in the first two or three weeks after the young hatch (Brisbin, 1969). In this case, the weight changes correlated with changes in total body water content, not fat content, and Brisbin suggested that this reflected a general hydration of body tissues as a water store to produce crop milk.

Breitenbach and Meyer (1959) and Breitenbach, et al. (1963) have thoroughly analysed weight changes during reproduction in the Ring-necked Pheasant. In the first study various organs were weighed during the laying period, after 20 days of incubation, and after 11 days of brooding; and in nonbreeding birds in reproductive condition (Table 29). The most drastic changes occurred in visceral organs

TABLE 29

Organ Weights of Adult Ring-necked Pheasants During Laying, After Incubation, After Brooding, and in Nonbreeding Individuals (from Breitenbach and Meyer, 1959).

Component	Weight in layers (g)	Percent difference from layers		
		Incubation	Brooding	Nonbrooders
Total weight	975	-19	-21	-10
Eviscerated weight	695	- 9	-10	0
Visceral fat	18.0	-81	-83	-51
Fat strip	3.0	-79	-87	-53
Ovary	24.4	-95	-97	-98
Oviduct	22.9	-89	-94	-93
Liver	24.1	-40	-51	-38
Intestine	23.3	-26	-37	- 5
Gizzard	15.9	- 3	-24	- 9
Kidney	7.3	-29	-28	-19

during the incubation period. The ovary and oviduct atrophied and most of the fat reserves disappeared, but relatively large changes also occurred in other visceral organs. The facts that eviscerated weight was almost 10% lower in birds after incubation than in nonbrooders, and that fat, liver, intestine, and gizzard weights were also lower, suggests that Ring-necked Pheasants tolerate decreases in organ function and energy reserves in order to incubate their eggs and brood their young. A weight loss of 19% (183 g), at perhaps 2.5 kcal/g, releases over 450 kcal of energy representing 600-700% BMR. This could conceivably represent 5-10% of the total energy requirement during the incubation period, an amount that might allow a one or two egg increase in clutch size.

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The degree to which pheasants will accept a loss of body weight for the sake of reproduction was demonstrated by Breitenbach, et al.'s (1963) experiments on the effect of reduced dietary intake on reproduction. Experimental birds were maintained on prereproductive levels of food intake (45-50 g/day) while control birds were allowed to increase their food intake. During the period of egg laying the weight of control birds increased 18% and their food consumption increased by 39% to 70-75g/day. But even though total body weight of experimental birds did not increase, the weights of reproductive organs increased by about the same amount as in control birds (Table 30). Normal eggs

TABLE 30

Weight of Organs in Ring-necked Pheasants During Prereproductive (February) and Reproductive (May) Conditions (after Breitenbach, et al., 1963).

Component	Control birds ¹ (ad libitum)			Experimental birds ² (limited intake)		
	Feb.	May	% increase	Feb.	May	% increase
Body	936	1,153	23	872	855	−2
Liver	16.7	28.1	68	21.3	26.3	23
Intestine	15.8	23.2	47	15.9	19.4	22
Ovary	0.39	28.9	7310	0.41	20.1	4802
Oviduct	0.54	23.8	4307	0.56	18.1	3132
Visceral Fat	15.2	50.1	230	2.16	5.6	159

¹Based on means of 5 birds.

²Based on means of 6 birds.

were produced, although fewer were laid (7.5 eggs/experimental bird compared to 84 eggs/control bird).

Under conditions of limited food intake pheasants evidently preserve their ability to reproduce at the expense of some impairment of maintenance function. Sudden release of dietary restriction quickly results in the resumption of normal egg production by domestic fowls (Heywang, 1940). Consequently, retention of egg producing ability through periods of unseasonably poor food supply appears to be a good strategy. Decrease in the ratio of female to male California Quail in southeastern Washington (Anthony, 1970) suggests that the physiological strain of egg laying may have increased the mortality rate of females. In samples taken at the end of the breeding season, the ratio was 0.95 in juveniles (birds of the year), 0.76 among one-year old

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birds, and 0.53 among older birds. These data suggest that females have 20-30% lower annual survival rates than males. Survivorship of females has also been found to be somewhat lower than that in males in Brown-headed Cowbirds (*Molothrus ater*) (Fankhauser, 1971) and Starlings (Kessel, 1957; Davis, 1959; Frankhauser, 1971). Coulson (1960) attributed a rather sudden change of the sex ratio in Starlings, favoring males after the first breeding season, to a greater incidence of breeding in first-year females than males. Kluijver (1952) found that while adult Great Tits lose weight while feeding young, adult survival appeared to be unrelated to brood size, and presumably then to the level of reproductive effort. Further studies relating survivorship to reproductive performance should be pursued, particularly in experimentally manipulated situations. Only in this way will the demographic consequences of reproductive effort be elucidated.

INTERACTION OF MOLT AND REPRODUCTION

The energetics of molt have been treated in this symposium by King, and elsewhere by King and Farner (1961) and Payne (1972). Since the relationship between molting and breeding season has been the subject of so much recent discussion in the literature (e.g., Fogden, 1972; Foster, 1974, *in press*; Miller, 1961; Moreau, Wilk, and Rowan, 1947, Payne, 1972; Snow and Snow, 1964; Ward, 1968), it seems worthwhile to discuss this subject briefly in terms consistent with the rest of this review.

Virtually every conceivable pattern is apparent in the timing and sequences of molt in birds (Stresemann and Stresemann, 1966). These patterns adequately demonstrate both that molt and other annual cycle activities compete for allocation of time (and perhaps of energy), and that the scheduling of molt is evolutionarily sensitive to a variety of considerations, including the morphology and behavior of the species and seasonal changes in its environment. In small altricial land birds, the only group that I will consider here, adults usually undergo a complete molt following, but not overlapping with, the breeding season. Molt lasts anywhere from two to four months in temperate region species and up to five months (Snow and Snow, 1964) or longer (Fogden, 1972) in the tropics. Furthermore, considerable overlap often exists between molting and breeding in tropical species with long breeding seasons (Ward, 1969; Payne, 1969; Moreau, 1936; Foster, 1974, *in press*). Ward (1969) and Fogden (1972) have suggested that breeding seasons in southeast Asian birds are attenuated to allow sufficient time for molt before annual periods of low food availability.

The cost of replacing feathers cannot be measured accurately in birds because changes in body conductance and activity patterns accompany the molt cycle. Measurements of metabolism during molt cycles have shown that birds typically increase metabolic levels by 10-30% (Wallgren, 1954; Perek and Sulman, 1945; West, 1960; Blackmore, 1969; Lustick, 1970; Payne, 1972). Koch and DeBont (1944) found that a

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Chaffinch (*Fringilla coelebs*) increased its energy expenditure by 25% while the flight feathers were being replaced but before body plumage molt had been initiated. This observation led King and Farner (1961) to suggest that increased conductance might be partially responsible for the increased energy expenditure during molt. Higher conductance would reflect the heat loss from the feather pulp, which contains the blood supply for the developing feather (see Lillie, 1940). Reduced insulation during molt is also commonly regarded as a cause of increased metabolism (e.g., Sturkie, 1954). Adelie Penguins seek sheltered places on shore and do not feed during their three week molt period (Penney, 1967). Heat loss to cold water evidently would be too great at this time to permit normal foraging. That energy expenditure during molt increases when measured within the thermoneutral zone in many species poses a difficulty for such heat loss arguments, but the hypothesis is consistent with correlations between feather growth, development of temperature regulation, and basal metabolism levels in growing birds (see pages 235-239). Impaired flight performances has also been cited as a possible cause of nonoverlap of breeding, molting, and migration (Stresemann and Stresemann, 1966).

King and Farner (1961) estimated the energy requirement of feather production during molt by House Sparrows as 7.6% of metabolized energy, assuming a 5.5 kcal/g. equivalent of feathers, 1.7 g of feathers produced in 60 days, and a 10% efficiency of feather production. Turcek (1966) determined that plumage weight (P) is related to body weight by the equation

$$P = 0.09 W^{0.95}$$

where P and W are expressed in grams. Thus plumage weight can be converted to % daily BMR in passerines by the equation

$$P = \frac{5.5 \times 0.09 W^{0.95}}{24 \times 0.031 W^{0.726}} = 0.651 W^{0.224}$$

where 5.5 is the energetic equivalent in kcal/g of keratin and the denominator contains Aschoff and Pohl's (1970) formula for BMR in kcals/hr, multiplied by 24 hrs. Thus body plumage represents 109% daily BMR in a 10-gram bird, 182% daily BMR in a 100-gram bird, and 306% daily BMR in a 1,000-gram bird. The actual cost of producing feathers depends on the duration of the molt period and the energetic efficiency of feather growth. If a 20-gram sparrow produces feathers equivalent to 127% daily BMR in 60 days (which represents quite rapid molt) at an energetic efficiency of 75%, the average energy expenditure above nonmolting conditions would be 2.8%. At efficiencies of 50% and 25%, energy expenditure would be increased by 4.2% and 8.5%, respectively. These values represent maximum estimates for birds weighing 20 grams and seem to attribute rather insignificant direct costs to molt.

Total protein limitation is also not likely to be caused by molt. If

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molt requires 2% BMR in protein accumulation, with a peak of perhaps 5% BMR, the maximum possible required ratio of protein/BMR (grams/kcal) is less than 0.01, which can be supplied even by a pure fruit diet (see Table 2). Requirements of particular amino acids needed for feather growth may impose more stringent limits but without further evidence it seems unlikely that protein availability is a major determinant of molt schedules, contrary to Ward (1969) and Fogden (1972).

DISCUSSION

The main body of this paper sought to identify and quantify components of avian reproductive cycles in energetic currency. The many gaps in our knowledge and understanding of this subject will have to be filled by future measurement and experimentation. But a broader and more basic question confronts us in this discussion, namely "What role have energetic considerations played in the evolution of the strategies of reproduction in birds?" Energy is a fundamental measure of biomass and activity, and management of energy resources must therefore be a primary problem of evolving systems. But we do not yet understand the adaptive significance of diverse reproductive patterns in any profound way.

"Adaptive significance" covers statements about the fitness of a prevalent trait relative to the imagined fitness of alternative traits that do not occur because they are, or would be, less fit than the prevalent trait. Most "adaptive significance" studies attempt to demonstrate why a particular characteristic is a superior evolutionary strategy. We should be sufficiently convinced of evolution by natural selection to accept this premise of "adaptive significance" studies, but the approach has been applied too narrowly to the evolution of clutch size, growth rate, and related characteristics. The components of the reproductive cycle are intimately tied to each other and to other phases of the annual cycle. One cannot study one aspect of the reproductive cycle independently without first determining its independence; components of the reproductive cycle are clearly interdependent.

To understand the diversity of reproductive patterns we must begin with the life table itself and assess the influence of changes in reproductive strategies on fecundity and mortality. The essence of this approach is contained in the complete life history model of a species, including the interaction of each component of the model with the environment. We are clearly not yet ready to construct such a model, but we can begin to outline the model and to describe some of its components.

The most fit reproductive pattern is that which enables its bearer to leave the greatest number of descendants over a given period; fitness must therefore be defined in terms of age-specific fecundity and mortality schedules. These factors enter into the equation for fitness in such a way that age at first reproduction and life expectancy influence

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fitness as strongly as fecundity does. The fecundity of a pair of birds during one breeding season may be defined as

$$\text{Production} = (\text{clutch size}) \\ \times (\text{survival to independence}) \times (\text{number of broods})$$

Whether the production of young influences the age at first reproduction directly is not known, but fecundity and life expectancy are closely linked through the level of reproductive effort of the adults (Williams, 1966; Gadgil and Bossert, 1970). Here we shall assume that an optimum level of reproductive effort exists for each species and that the time and energy available for reproduction are fixed. We must now ask how birds can best use this time and energy for the production of young.

We must keep four principles in mind. (1) Time and energy must be thought of as being equivalent. Energy influences reproduction by its rate of use, that is, energy per unit of time. The time adults can forage determines the amount of energy they can gather; time spent brooding detracts from time spent foraging; the length of incubation absences determines the loss of heat from the eggs; time spent flying between the nest and the feeding area is unavailable either for direct parental care or foraging. Time and energy can be equated by a suitable conversion factor.

(2) Energetics can be related to evolutionary fitness by the influence of patterns of energy use on fecundity and survivorship. Suitable conversion factors must be found to equate energy and fitness. In some cases, it is sufficient to know whether a change in energy use has an increasing or decreasing influence on fitness. But changes in energy use frequently influence many components of fitness in opposite directions, in which cases it becomes mandatory to quantify the relationship between energy and fitness.

(3) The components of the equation for fitness are not independent. Changes that principally effect one aspect of reproduction influence all others and require a total readjustment of the reproductive strategy to attain a new optimum. A change in nest construction alters the rate of predation and the rate of heat loss from the nest, altering in turn the optimum duration of parental care after fledging and both the percent of time spent incubating and length of incubation absences. Increasing distance to the feeding area may reduce the total time spent foraging and select for greater thermal independence of the nestlings, altering in turn the number of young raised and their rate of development.

(4) Adults and young must be treated together as a unit of energy use. Adults must allocate their resources not only between their own functions, but also between themselves and their young. Any change in the use of energy by the young must affect the budgeting of energy by their parents.

It would be pointless to attempt to construct a complete model of the reproductive strategy. In the following sections, we shall consider

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some aspects of reproductive strategy and the environmental factors that influence them.

ENERGY EXPENDITURE BY ADULTS AND CLUTCH SIZE

The rate at which energy can be made available for reproduction is limited by the ability of adults to mobilize and expend energy. Energy requirements above maintenance levels that are imposed upon adults by reproductive activities during each stage of the nestling cycle in typical passerine and galliform species are summarized in Table 31.

TABLE 31

Energy Requirements (%BMR) of a Typical Passerine and a Typical Galliform Species, as a Function of Stage of Nest Cycle.

Stage	Passerine	Galliform	Source
Ovarian and oviducal growth	2-12	3-10	Table 6
Egg formation	45	126	Table 11
Incubation ¹	25-50(100)	(50-100)	Table 17; Fig. 8
Nestling ¹	200-300 ²	—	

¹Requirements of the pair.
²Based on a pair feeding four young with a peak energy requirement of 100-150% BMR per nestling.

In preparing this table I assumed that during foraging adult birds gather about three times as much energy as they expend. This index of foraging efficiency is 2.5 for Mangrove Swallows calculated from estimates in this paper for high food availability. Indices for nectar feeding species are about 2.5 for hummingbirds, and 4.0 for sunbirds (Wolf, Hainsworth, and Gill, MS). With an index of 3, an adult spends half again of the food energy it can deliver to its young to gather the food. Thus 100 kcals delivered to young represents 50 kcals of energy expenditure by the adult for foraging.

Energy expenditure for gonadal growth and egg laying in songbirds apparently exerts little energetic strain on adults, particularly since neither activity restricts potential foraging time. Galliforms require more energy for egg production than passerines because their eggs are larger and have a greater energy density. Egg production evidently adds almost 200% BMR to the energy budget of the female galliform, which is apparently more than the added expenditure for incubation. Egg production would not set the ultimate limit to fecundity in galli-

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forms unless egg laying creates an energy or nutrient deficit. Clutch size increases each day egg laying is prolonged; lengthening the combined laying and incubation periods to increase clutch size would increase the risk of mortality from predation. But if a nest has a mortality rate of 0.04, for example (Ricklefs, 1969b), over a period equal to the interval between eggs, increasing clutch size by an egg would more than compensate this loss up to a clutch of 25 eggs. Lack (1967) has suggested that because ducks laying large eggs relative to body weight tend to have small clutches, clutch size is limited by the ability of the female to form eggs. The fact that ducks have the highest energy requirement for egg formation of the major groups surveyed (180% BMR compared to 126% BMR for galliforms; Table 11) lends credence to Lack's hypothesis, although one must further demonstrate that laying puts the female into an energy or nutrient deficit.

The most likely limit to the fecundity of galliforms would seem to be the number of eggs that adults can incubate. But the incubation energy requirement seems to be little more than the laying requirement, even considering that foraging time is curtailed by incubation. Moreover, several studies have shown that precocial species can successfully incubate larger than normal clutches (Klomp, 1970; Wynne-Edwards, 1964; Hilden, 1964).

Estimates of energy expenditure in passerines do not distinguish clearly the stage of the nest cycle during which fecundity is limited. Incubation requirements, including increased energy expenditure for foraging, could vary between 37 and 75% BMR with an extreme of 150 BMR possible. At their peak energy requirement, young demand 200-300% BMR of their parents (both parents feeding four young), but only 100-150% BMR, that required for foraging, must be metabolized by the adults. This would still appear to be more than the requirement for incubation in most species, perhaps excepting arctic species with large clutches. Hussell's (1972) experimental demonstration that Snow Buntings can raise larger than normal broods may indicate clutch size limitation during the incubation period. Indeed, a fruitful approach to the problem of clutch size limitation would include extensive experimental manipulation of clutch and brood size, combined with measurements feeding rates and weights of adults and young.

MODE OF DEVELOPMENT

Patterns of development in birds vary between extreme precocial and altricial conditions (Nice, 1962). Independence is the key to developmental pattern; precocial chicks (e.g., galliforms, anseriforms) are nearly self-sufficient at hatching and quickly develop adult levels of homeothermy and mobility. Newly hatched altricial birds depend upon their parents for body heat and food. Temperature regulation and feeding are acquired by altricial species after they have attained body weights close to those of adults.

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Precocity of development is related primarily to the type of food exploited by, or fed to the young. All self-feeding precocial species utilize resources that require relatively little strength or skill to obtain: usually vegetation, seeds, or insect larvae, and that are found on the ground or benthos of an aquatic habitat. Flying and swimming prey are too difficult to catch; branches and foliage require too much skill to negotiate. If these prey are to be food for young, they must be captured by adults and delivered to the young.

If a prey resource can be exploited by young birds, selection will seemingly always favor precocial development because self-feeding increases the number of young that can be raised. Except for shorebirds, precocial species raise more young than altricial species and mortality probably does not differ greatly from that of altricial young (Ricklefs, 1968, 1969b). If the young must be fed by their parents, energetic efficiency may favor altricial development and the resulting rapid growth rate may shorten the development period and thereby reduce exposure to predation. Poikilothermic nestlings huddled together in a well-insulated nest may lose heat slowly enough compared to the same number of free-roaming homeothermic young to offset the loss of feeding time because of brooding. Furthermore, altricial nestlings begin to develop homeothermy, and thereby release parental brooding time, before they reach their peak energy requirement.

The relationship between growth rate and precocity of development has been described by Ricklefs (1973a). Although most precocial species grow slowly, presumably because most of their tissue is fully mature and not capable of embryonic function, homeothermy is maintained by many anseriform and charadriiform chicks without noticeable slowing of growth. The degree of muscular development required to provide adequate thermogenesis for temperature regulation may not require such commitment to mature function that growth is slowed. In fact, none of the rapidly growing precocious species develops flight at an early age (e.g., gulls, terns, and pond ducks).

Gull, tern, and alcid chicks have retained homeothermic potential from hatching, while being fed by their parents. One may argue that thermoregulation and the downy condition at hatching characterize the order Charadriiformes, which includes precocial species, and that the habit of self-feeding is more recently derived, or that larid evolution is too conservative to have led to an altricial condition. Although precocity of development tends to be uniform within families or orders, the Laridae is an old, diverse group within which evolution has almost certainly had ample time and opportunity to modify development. If clutch size in the Laridae were limited at some time other than the nestling period, selfsufficiency of the young would influence fecundity little and lack of brooding could free the adults for other activities during the early part of the nestling period. Experiments with increased brood size indicate that gulls can raise larger than normal broods (Harris, 1964; Harris and Plumb, 1965). The num-

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ber of young raised by gulls and the type of nest construction also may not be such to favor energetically keeping the young together in a nest. Predation may favor mobility, which would tend to minimize total losses of broods.

The homeothermic condition of young petrels, and undoubtedly of other procellariiform birds, deserves special attention. Adult petrels feed at a great distance from the nesting site, requiring considerable nonproductive traveling time, and incubation spells are correspondingly long. Continuous brooding of the single chick would completely prevent one adult from feeding and therefore reduce foraging capacity by half. In most species of altricial birds, parents brood their young for a relatively small portion of the day, even on the day of hatching, and so brooding reduces feeding potential by less than 50%. In petrels early development of homeothermy frees both adults to forage full time (the young are brooded for only a few days after hatching). Homeothermy in the cold (10-15°C) environment of the petrel chick has forced an early maturation of the integument (insulation) and musculature (heat generation). In terms of water content of tissues (low in mature tissues) and similarity of body proportions to adults, petrels have the most precocious development of any species I have examined, including terns and quail, although they are among the most inactive nestlings I have ever seen. Slow growth of petrel chicks may be a direct consequence of their precocious development.

RATE OF GROWTH

Most variation in growth rate among species of birds is related to adult body size and precocity of development (Ricklefs, 1968, 1972). The general decrease in growth rate, expressed as a percent of adult weight, with increasing adult body weight still defies explanation, as do many relationships between physiological function in adults and body size (see the paper by Calder in this volume). I have discussed the inverse relationship between precocity of development and growth rate elsewhere (Ricklefs, 1972). My general thesis is that maturation of function in tissues occurs at the expense of embryonic capacities, and that the tissue of precocial species are physiologically incapable of more rapid cell proliferation and growth, regardless of their state of nutrition. If this were true, growth rate would be tied more closely to the evolution of precocity than to energetic considerations. For discussion of the energetic efficiency of growth see Blem (1973), Brisbin (1969), Diehl and Myrcha (1973), Kahl (1962), Koelink (1972), Myrcha, et al. (1972), Penney and Bailey (1970), and Westerterp (1974). Energetic efficiency among birds of similar body size is determined largely by rate of growth; efficiency will not be considered here because I believe it is not a primary influence on the evolution of reproductive patterns and because its measurement depends on an arbitrary definition of the length of the development period. For discussion of the energetics of growth as a part of the total energy flow

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of a bird population one may consult Kale (1965) and Pinowski and Wieloch (1972).

Two groups of birds exhibit slower growth than one would expect on the basis of their mode of development: seabirds that raise only one young (Ricklefs, 1968; Ricklefs and White, unpubl.) and tropical songbirds (Ricklefs, 1968, MS; White and Ricklefs, unpubl.). To argue that availability of energy limits growth rate in these species, one must demonstrate that growth rate could affect the limiting energy requirement of the young. The Sooty Tern grows about as rapidly as possible without increasing the maximum energy requirement of the young (see Fig. 25), suggesting that the hypothesis of an energetic limitation to growth rate in this slowly growing, tropical seabird is plausible. Most slowly growing seabirds exhibit a Gompertz form of growth curve with an early inflection (point of maximum growth rate), which increases the overall efficiency with which growing chicks can utilize a constant energy source (see Fig. 29).

Most rapidly growing seabirds inhabit cold water areas where the energy demand of temperature regulation increases the energy requirement for maintenance. Under these circumstances growth energy requirements can be relatively large before they increase the maximum energy requirement of the young (see Fig. 29). For example, Common Terns grow twice as fast as Sooty Terns, but their maintenance energy requirements are also about twice as high, primarily because Great Gull Island, where Common Terns breed is considerably colder than the Dry Tortugas, where Sooty Terns breed (Ricklefs, Cullen, and White, unpubl.).

One could extend this efficiency-optimizing argument more generally to growth rates in all altricial species, but supporting evidence is indirect and does not make this hypothesis any more convincing than the growth rate-maximizing hypothesis mentioned above (Ricklefs, 1969, 1972). However, if growth rate has evolved to minimize the maximum energy requirement of the young, and therefore if growth rate is closely tied to maintenance energy requirements, an explanation for the relationship between growth rate and adult body would size follow directly. Growth rate in altricial land birds declines with increasing body weight at the same rate as basal metabolism rate, expressed on a per gram basis.

Can the energy-minimizing hypothesis account for the observation that growth rates in tropical songbirds are about one-quarter less than those of temperate and arctic species? In fact, standard metabolic rates of tropical nestlings are about one-quarter less than those of temperate species (Ricklefs, MS; White and Ricklefs, unpubl.), which is consistent with the hypothesis. The reduced metabolic rates of tropical birds during the growth period may be tied to plumage development. If tropical nestlings grow fewer feathers than temperate nestlings or delay the growth of some plumage elements, the decrease in heat loss through developing feather quills would permit decreased standard

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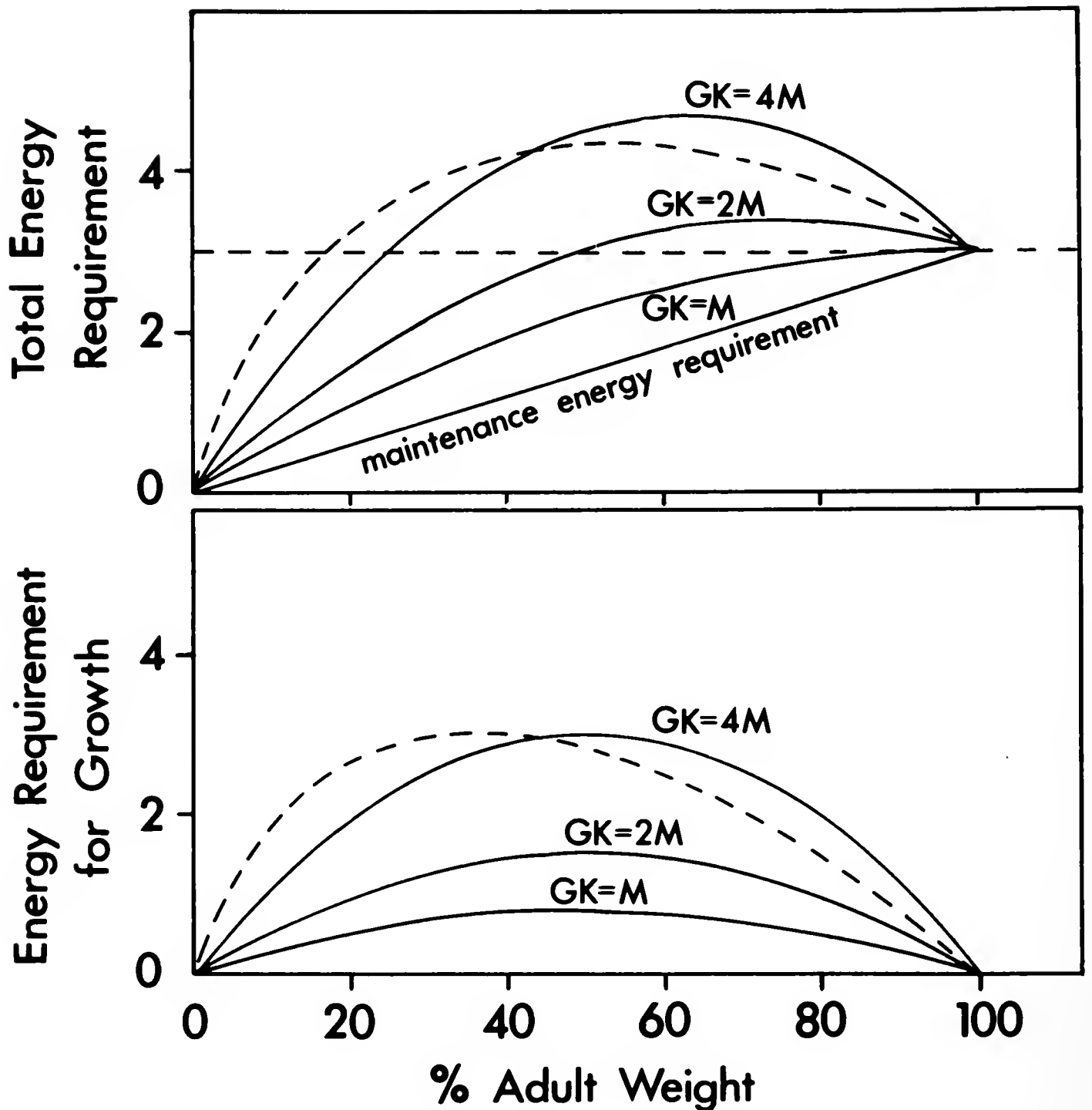


FIG. 29. Influence of growth rate on the total energy requirement of young. K = growth rate constant of the logistic equation; G = energy density of tissues (e.g., kcal/gram); M = metabolic rate of the young (e.g., kcal/g·day). Growth energy requirement does not raise the total requirement of the young above the maximum maintenance requirement of the young when $GK \leq M$ (see Ricklefs, 1969, MS). A growth curve of Gompertz form shifts the growth energy requirement curve to the left and reduces the total energy requirement of the nestling without a change in the overall growth rate (dashed line).

metabolism. Metabolic rates are, in fact, lower in tropical species than in temperate species. But if the “quill hypothesis” is responsible for this difference, standard metabolism in the thermoneutral zone must consist largely of heat production to maintain body temperature and birds must control their body temperatures in the “thermoneutral zone” by manipulating physical pathways of heat loss to balance this excess heat production. The nature of basal metabolism is beyond the scope of this paper but indirect evidence relating heat production in nestlings to feather development (see Figs. 15-22, 27) suggests that this hypothesis should be pursued further.

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DISCUSSION

WILLIAM R. DAWSON: I've asked Dr. Odum to initiate the comments here. Before he does so, I'd like to attest to the problem that Dr. Ricklefs has had in keeping his remarks within the allotted time. He has really produced a monumental synthesis in the manuscript

version of his presentation, and what you have heard is an abstract, which I think gives you some glimpse of some of his concerns. I think his contribution is destined to be widely cited, particularly because much of the information assembled in it is drawn from sources that are not readily available to the ornithologist.

EUGENE P. ODUM: It's a great pleasure to comment on this paper, and the manuscript. I'll certainly reaffirm what the chairman said, that this is a monograph of real dimensions, and I will certainly agree that the paper will be widely quoted. It's full of tables and data that we'll all want to use; the whole 200 plus pages of the manuscript are full of fascinating material.

I am sorry that Ricklefs didn't have time to show his summary slide of altricial development because I believe that there may be a parallel between the development of altricial birds and the current development of fuel-powered human society. At least, man seems to be following the altricial model rather than a precocial one. Man's present preoccupation is with an embryonic-type growth fed by energy exploited from fossil fuels is much like the rapid early growth of noisy nestling birds clamoring for ever more food from hard-working parents. In the altricial model as much as possible of the energy input goes at first to growth, and only later in development comes the shift to maintenance and quality control necessary for maturity. In the precocial model quality development goes along with growth so the overall rate of growth is slower at first. The altricial strategy pays off so long as there is a period of surplus energy. Most altricial species time their breeding to coincide with seasonal abundance of insects, seeds, fruit, or whatever provides the major source of energy. It is thus quite appropriate for human society to adopt this strategy when there is a temporarily unlimited energy supply, as in the case of fossil fuels, but ultimate survival also depends on ability to shift rapidly from growth to maintenance when energy supply decreases, or when other limitations to growth in size appear. So far man has shown an awareness of the danger of continuing too far with embryonic-type growth (where mouths and stomachs are the input organs) but he has not yet seriously thought about what economic and social changes will be necessary to phase into maturity.

The only other point that I would like to make a quick note of is the question whether or not the heat generated for temperature regulation is enough to incubate the eggs, so that you don't have to add incubation as an energy cost in your budget. This is interesting in terms of proposals for using waste heat for useful purposes and thereby reducing or making more efficient energy consumption. Let me point out that possibilities along these lines depend on the quality rather than quantities of energy. A calorie of heat is not the same as a calorie of food when it comes to getting work done. Without getting into thermodynamic terms at all, we might just say that there's high utility energy, and there's low utility. There's a lot of energy in the sun, but most of

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it is low-utility, so we can't use that low-utility energy to run a city, or automobiles, or other high powered machinery without some kind of expensive concentrative mechanism. So I think we must determine what is the quality of the energy radiated from the body. It may be so low in its utility, that is, too dispersed in a thermodynamic sense to keep the temperature of the egg at the proper level, although it might help. On this basis it would be well to assume that some extra energy from food or fat is required for incubation until the matter is studied further.

DR. DAWSON: Dr. Odum obviously has struck a responsive chord. I noticed a lot of people with late-model large cars with emission control on them were leaning forward hoping to find out how to get more mileage than they currently are. Perhaps we could talk him into giving us a seminar this evening coupling birds and the energy crisis. What I would like to do is offer Dr. Ricklefs the opportunity to respond if he cares to. I don't think there's much controversy there to deal with, but if you want to add anything to Dr. Odum's comments please feel free to do so.

DR. RICKLEFS: I would like to point out only that Gene's argument that altricial development necessarily leads to rapid growth and early death is not supported by the observation that many long-lived birds—albatrosses and eagles, for example—exhibit altricial development. Gene's style of armchair philosophizing is probably more entertaining than of relevance to either avian energetics or to the development of human societies.

DR. ODUM: I'd like to go back to something that was said regarding proportioning of energy and length of life. Of course, you can't have everything; if you go for high growth, you also go for low quality, but this does not necessarily preclude long life. If a period of rapid growth is followed by a longer period of mature growth, then a longer life can be assured. This is perhaps what happens in the case of the albatross. In the analogy with cities, those that grow too fast can't maintain their structure or take care of wastes. The taxes get so high that the city is faced with disorder and decay unless energy flow is reordered for maintenance. It's not so much a matter of the time scale as it is the shape of the growth curve, that is, whether the boom is followed by a bust, or by a reordered period of steady state.

DR. DAWSON: Perhaps you might wish to comment, Dr. Kendeigh.

S. CHARLES KENDEIGH¹: Dr. Ricklefs has an exhaustive presentation

¹ For the convenience of the reader, Dr. Kendeigh has elaborated on his oral presentation and also included references to pertinent literature.—Ed.

and has treated many subjects well. I have a few miscellaneous comments.

Metabolizable energy of foods.—Dr. Ricklefs mentions that efficiencies of food assimilation vary tremendously with the organism, the nature of the food, and ecological conditions. He does not discuss it further, but I wish to emphasize its importance if we are to evaluate different kinds of foods for birds and the impact that birds make in ecosystems.

We have measured the metabolizable energy coefficients for a number of different species and find it to vary from 62 to 80 per cent, even when using exactly the same kind of food. Further, the coefficient may vary in the same species when consuming different kinds of food; for instance, in the House Sparrow, 67 vs. 81-87, when feeding on two different chick mash diets.

We need determinations of metabolizable energy coefficients on all sorts of natural foods of birds. Only a few such measurements have been made. The experimental procedure is relatively simple but requires some special equipment, space, time, and effort.

Resting, standard, and basal metabolism.—This paper and others given in this symposium call to mind that we need to be careful in the use of terms relating to metabolic state to avoid confusion or misunderstanding. *Resting metabolism* is the rate of energy utilization of birds at rest, but digesting and assimilating food. *Standard metabolism* is the rate of energy utilization of birds at rest in a fasting condition. *Basal metabolism* is standard metabolism measured in the zone of thermal neutrality, preferably at night.

Rubner's principle of compensation.—Rubner may have alluded to the possibility that the heat liberated by exercise substitutes for part of the increased tissue metabolism required in inactive animals at low temperatures, but his chief attention was given to the role played by the heat increment of feeding. I think he has clearly shown that this heat is compensatory at low temperatures in mammals, and there is every reason for believing this is also true with birds. This is a problem, however, that needs to be investigated with birds in a comprehensive manner.

The heat or energy generated by moderate activity is often additive to standard metabolism at low temperatures, rather than compensatory, as Bob stated. However, some work with rodents indicates this relation varies with species, how they are acclimatized, and the ambient temperature (Jansky, 1965). More work also needs to be done on this point.

Death at low temperature.—Bob states that existence at extreme low ambient temperatures may be limited by the heat generating capacity of the muscles rather than the ability to assimilate energy from ingested food. I have no firm conviction one way or the other on this point. Sometimes birds die at low temperatures with fat deposits still present on the body. On the other hand, it is very common to note the gradual

decrease in weight of birds at these extreme temperatures before they finally succumb. In these cases, it appears that they are using energy at a faster rate than they are able to replace it.

I should point out that the maximum rate of energy mobilization that determines the lower limit of temperature tolerance is, as we have measured it, the sustained rate over 24 hours, day after day. It is the maximum rate of energy use that can be replenished through feeding without loss of weight to the bird. This is quite different from the rate, 6-16 times basal metabolism, obtained in bird flight. This energy is expended only for periods of minutes or sometimes hours, and the energy debt is repaid during more leisurely activity the rest of the day.

Productive energy and egg production.—I am very much interested in the evidence Dr. Ricklefs brings together showing that deprivation of food intake may bring a reduction in egg production. The basic theme that our group has been working on is that the activity of birds and other animals is conditioned by the amount of productive energy that they have available. When this productive energy is not available in adequate amounts, the activity is delayed or curtailed.

Egg temperatures.—Egg temperatures vary with their position in the nest. J.A.L. Mertens, in Netherlands, is showing that there may be several degrees difference between the temperature of an egg in the middle of the clutch and an egg on the outer edge, in large clutches. It is important that the bird's activities in the nest shift the position of the eggs at frequent intervals so that they all maintain an equal temperature throughout incubation and thereby a uniform embryonic development. We need more observations on how this is accomplished.

Cooling rates of eggs.—It is very desirable to measure the cooling rate of whole clutches of eggs as well as of single eggs. If the cooling rate of whole clutches, together with the nest, could be determined at different ambient temperatures, then my equation (Kendeigh, 1963) for calculating the energy cost of incubation could be simplified by using ambient temperature instead of nest temperature.

Cooling rates of eggs depend in large part on the insulative efficiency of the nest. This latter depends on how it is constructed, the materials of which it is made, and where it is located. This is a relatively untouched area of research and attention to it should yield some interesting and worthwhile results.

Energy cost of growth in young.—Bob's curves showing energy requirements in young for growth and maintenance are very interesting. They do not show, however, daily energy cost of growth or the total energy required for growth from hatching to independence out of the nest. This requires a time scale on the horizontal axis of the figures. If this were done, one could then add up kcal/day on the vertical scale to obtain the total. We need such data to add to the energy requirements of adults, in estimating the impact of a species in its ecosystem.

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DR. DAWSON: Dr. Bartholomew has indicated that he has a few brief, very brief, remarks.

GEORGE A. BARTHOLOMEW: I shall confine myself to a single point, and that is this: Whether you in this audience realize it or not, the three papers that have so far been presented, when published, will represent the base line from which all subsequent studies involving the energetics of birds must start. This will have a very strong and positive effect on the quantitative aspects of data acquisition by ornithologists, because one simply cannot afford to operate below the state of the art and the state of the art has become fairly advanced in avian energetics as you can clearly see.

One of the points that is quite obvious from this, is that in addition to the precept which Dr. King enunciated earlier—that we must deal with energy, space, and time—there is a fourth category which was implicit in what Ricklefs said, namely the category of materials, which can never be ignored.

This brings us to what for me is a morass, namely biochemistry. But, the fact is that to extend our insights into evolutionary strategies of birds particularly with regard to growth and reproduction, we must include good analytical chemistry. Fortunately, this is less formidable than it would have been 15 years ago, not because people are more intelligent, but because there are reliable physical instruments which allows us shortcuts to chemical analysis. As a non-chemist I am almost reluctant to say this, but the future really invites careful quantitative chemistry to fill in the fourth category in the general framework of avian energetics.

ENERGETICS OF NATURAL AVIAN FLIGHT

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INTRODUCTION

How much energy must a bird use to fly? This question has intrigued ornithologists for decades, and many estimates are available (for reviews, see Tucker, 1971; Hart and Berger, 1972; Tucker, 1972; Bernstein, et al., 1973). Engineers who work with man-made flying machines rather than birds rephrase the question "How fast will this aircraft use fuel?" The answer is of considerable importance in this day and age and, not surprisingly, engineers have devised methods of estimating

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fuel consumption, even for a machine that exists only as a table of dimensions. The accuracy of these estimates is verified by direct measurements after the aircraft is built.

The fuel consumption of an aircraft depends on many variables and, fortunately, the theory relating these variables is general enough that one can apply it to flying birds (for example, see Pennycuick's theory (1969); and my modification of it (1973)). Data gathered on birds and bats flying freely in wind tunnels have made it possible to test predictions from theory, and many of the predictions are accurate within 10 to 20% (Tucker, 1973).

It is tempting to use the theory for birds flying in a wind tunnel to calculate the energy requirements of free-flying birds in nature, but two problems arise. First, it has not been possible in nature to measure accurately the vector velocities of the bird relative to both the air and the earth, and the theory cannot be evaluated without these data. Second, there are differences between the natural environment and that in the wind tunnel. These differences might make the predictions for the wind tunnel inaccurate for the natural environment. The magnitude of this second problem cannot be conclusively determined until the first problem is solved and simultaneous measurements of velocities and energy requirements are made. The prospects of achieving this in the next few years seem bright, given the present rate of development of technology.

For now, I will discuss the differences between the natural environment and that of the wind tunnel from the point of view of how these differences might influence the power requirements (i.e., rate of energy use) for avian flight. Then, anticipating the solution of the problems mentioned in the paragraph above, I will discuss the predictions the theory makes for the power requirements of avian flight at different altitudes and in different wind directions. Some of these predictions have been made before, either from theory (Pennycuick, 1968, 1969) or measurements (Tucker, 1971). The tested theory presented here makes these predictions on a sounder basis, and agrees in the main with this earlier work.

QUANTITIES AND UNITS

The quantities used in this paper are the conventional ones used by engineers. The terms "force" and "velocity" denote vector quantities which have both a magnitude and direction in space. All other quantities are scalars, having only magnitude. Power is the scalar product of force and velocity and has dimensions of energy/time. All quantities are given in the international (SI) system of units (Mechtly, 1969). Unless otherwise specified, mass is given in kilograms, length in meters, time in seconds, power in watts and speed in meters/second ($1 \text{ m/sec} = 2.24 \text{ miles/hour}$). Weight is a force given in newtons and is equal to mass multiplied by 9.81 m/sec^2 , the acceleration due to gravity.

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WIND TUNNEL CONDITIONS AND NATURAL CONDITIONS

BOUNDARY CORRECTIONS

In a wind tunnel of closed-throat design (which is the sort that has been used during measurements of gas exchange in flying birds), the air that flows around the bird is bounded by rigid walls. These boundaries produce extraneous aerodynamic forces that are not present in nature. The extraneous forces have been quantified for aircraft models and are predictable. The process of subtracting these forces from measured forces constitutes "boundary correction" and results in corrected wind tunnel data that predict the aerodynamic forces encountered in free air. The boundary corrections arise solely because the airflow around the model (or bird) is bounded in some fashion, and are not related to the fact that the model is stationary and the air is moving rather than vice versa. Aerodynamic forces are the same for a given relative motion between model (or bird) and air, whichever is taken as stationary.

The various sorts of boundary corrections are too numerous and complex to describe completely here (see Pope and Harper, 1966, for review). With one exception, all of them together will influence the power requirements reported here by less than 1.5%. The exception is the "down-wash correction." In a closed throat tunnel, the measured drag of an aircraft is too low, and the down-wash direction compensates for this. The down-wash correction would increase the power requirements reported here by less than 10%, and has not been made.

AIR TURBULENCE

If the air through which a bird flies has everywhere a constant velocity relative to the earth, the air is by definition nonturbulent. Air is seldom nonturbulent as it is continually stirred by convection currents with both horizontal and vertical components. The turbulence may be small-scale, i.e., the mean distance a bird travels without encountering a change in air velocity is, say, less than one-tenth of the wingspan—or large-scale, i.e., the mean distance a bird travels before it encounters a change in air velocity is greater than ten wingspans. Small-scale turbulence can have profound effects on the aerodynamic forces produced by aircraft wings, although the few measurements available for birds suggest that the power requirements for flight are not influenced greatly by small-scale turbulence (Tucker, 1972). The feather structure of birds also suggests that flight is not greatly influenced by small-scale turbulence (Tucker, 1972). The intensity of small-scale turbulence in the natural environment can be less than that in the wind tunnel, or can be much more, depending on conditions. I see no reason to expect that small-scale turbulence will cause differences in the power requirements of avian flight between the wind tunnel and the natural environment.

Large-scale turbulence is another matter. It does not occur in the

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wind tunnel but is common in nature. Wind gusts, up-drafts and down-drafts driven by thermal convection or surface features, wind shadows, and shear layers all may be classified as large-scale turbulence. Large-scale turbulence has profound effects on the power requirements for flight. In fact, soaring birds, by seeking out up-drafts and shear layers can remain aloft for hours without flapping their wings at all. Up-drafts and down-drafts that may be associated with large-scale turbulence can be duplicated in the wind tunnel, and their effects on the power requirements of flight will be discussed later.

DRAG AND WEIGHT OF APPARATUS ATTACHED TO THE BIRD

The mask (and the tube connected to it) that a bird wears in the wind tunnel adds aerodynamic drag. The masked bird must do extra work to overcome this drag force. The extra power required can be quantified (see Appendix), and is 10 or 20% of the measured values depending on conditions (Tucker, 1972).

In addition, the mask and tube increase the bird's weight by 3 or 4%. This weight increase could also increase the power requirements of flight for two reasons: (1) The bird must do extra work to support the weight, and (2) since the weight is added ahead of the center of lift, it will cause a pitching moment. The bird must compensate for this moment and do extra work in the process. The increases in power requirements during flight to support the weight of the mask and tube are in the range of 2 to 3%. To counteract the pitching moment, they are an order of magnitude less (see Appendix).

BEHAVIORAL EFFECTS

The above discussion considers all of the aerodynamic and mechanical differences that I can think of between a bird flying in a given configuration in a wind tunnel and one flying through an unlimited mass of still air at the same temperature, humidity, and pressure. However, a bird in a wind tunnel, perceiving that it is flying in an enclosed, noisy space, might as a consequence alter its power requirements from those required by the aerodynamic and mechanical properties of the environment. For example, it might drop its feet and spread its tail to a greater extent than in natural conditions. These changes could increase aerodynamic drag and the power requirements of flight. It is even conceivable that internal changes in metabolism could influence the energetics of flight without any overt changes in behavior. Is there any evidence that such overt and covert behavior causes the results from the wind tunnel to differ from what occurs in nature?

Overt behavior of birds flying in the wind tunnel does change from time to time in a manner that influences power requirements. For example, the metabolic rates of Laughing Gulls (*Larus atricilla*) flying in a wind tunnel under specified conditions may not stabilize for

15 to 20 minutes. During the first few minutes of flight, the metabolic rate may be 15 to 20% above the level at which it eventually becomes constant. This change in metabolic rate correlates with the observation that the gulls move about more in the tunnel during the first few minutes of flight than they do thereafter (Tucker, 1972). The gulls also may flap in the tunnel when they could glide, or may fly with their feet hanging into the slipstream. However, all of the results referred to in this study were obtained when flight was steady and had the same appearance as natural flight. Under these conditions, the standard deviation of the power required for flight by gulls was about 10% of the mean value. The standard deviation indicates the maximum effect of any remaining overt or covert behavioral changes between the experiments.

Budgerigars (*Melopsittacus undulatus*) flew in the wind tunnel with less variation in behavior and power requirements than Laughing Gulls. They flew steadily after the first few seconds, and their power requirements did not change significantly thereafter. In flight, they appeared identical to free-flying birds. From one experiment to the other the standard deviation of the power required for flight was about 5% of the mean value (Tucker, 1968).

Whatever behavioral peculiarities a bird might have in the wind tunnel, its flight at a given velocity has power requirements that must fall within minimum and maximum limits. These limits are set by aerodynamic, mechanical, and physiological considerations. It is useful to calculate the limits as outside values of the effect that unknown behavioral perturbations in the wind tunnel conceivably could have.

The theory that predicts power requirements for birds flying in the wind tunnel has only two parameters that have both large uncertainties in their values, and large effects on power requirements. These are muscle efficiency (E) and profile power. Muscle efficiency under flight conditions could vary from near zero to some maximum value. A generous estimate of this maximum value is 0.3. The highest efficiency usually considered for mammalian muscle is about 0.25, and the highest value that I know of for any muscle is 0.35 for an isolated tortoise muscle (Woledge, 1968). The theory for flight in its present form makes accurate predictions with an assumed value of 0.2 for muscular efficiency. If muscular efficiency approaches zero, the power requirements of flight approach infinity. As efficiency increases, power requirements decrease as will be discussed below.

The parameter "profile power" is a rate of energy expenditure associated with moving the wing, and cannot be as low as zero. However, if we assume that profile power is zero and that muscle efficiency has a maximum value of 0.3, we can calculate values for the power requirements of flight that are almost surely below anything that a bird conceivably could attain. These values are about one-third to two-fifths of those measured in the wind tunnel (see Appendix).

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SUMMARY OF DIFFERENCES BETWEEN THE WIND TUNNEL AND THE NATURAL ENVIRONMENT

For wind tunnel measurements used in a theoretical analysis of flight energetics, the foregoing discussion indicates that aerodynamic and mechanical differences between a bird flying in a wind tunnel and one flying through still air will cause a difference in power requirements in the two situations of less than 10%. The only correction required to achieve this level of agreement is a correction for the aerodynamic drag of the apparatus attached to the bird in the wind tunnel. There is no direct evidence to suggest that overt or covert behavioral peculiarities of birds flying in wind tunnels cause the power requirements of flight in a wind tunnel to differ from those flying through still air. If such peculiarities exist, they could cause the wind tunnel data to be either too high or low. In the former case, power requirements in nature of less than one-third to two-fifths of the wind tunnel measurements seem implausible.

THEORY

In the first section of this paper I compared flight in a wind tunnel with flight in nature through still air. The power requirements for flight in a wind tunnel are described with reasonable accuracy by a set of equations that constitute a theory (Tucker, 1973). My aim in this part of the paper is to generalize this theory so that it applies to flight at different, constant altitudes and in winds of different velocities. Altitude and wind velocity are both variables that influence the power requirements of natural flight.

The rate of change in wind velocity with respect to space or time is another variable that can influence the power requirements of flight. When a bird encounters such changes, it experiences acceleration in its air velocity and, consequently, changes in aerodynamic forces. If the bird maneuvers appropriately, it can use accelerations in its air velocity to reduce the power requirements of flight. An extreme example of this behavior is the dynamic soaring of albatrosses (Cone, 1964; Wood, 1973). The effects of acceleration on the power requirements of flapping flight are complex and incompletely analyzed, and I will not consider them in this paper.

The theory that predicts the power requirements of birds flying level in a horizontal air stream in wind tunnels divides and subdivides these power requirements into several categories that can be analyzed separately. The first division separates the power required by the flight muscles from that required by the rest of the bird. Then the muscle power (power output, P_o) is subdivided into three categories: (1) induced power ($P_{o, \text{in}}$), which supports the bird's weight, (2) parasite power ($P_{o, \text{par}}$), which overcomes the aerodynamic drag of the bird's body,

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and (3) profile power ($P_{o,pr}$), which is the muscle power in addition to (1) and (2) that is necessary for flapping the wings.

The power input required by the bird exclusive of the power input to the flight muscles also is subdivided into three categories: (1) the basal power or basal metabolic rate ($P_{i,B}$), which accounts for maintenance activities, (2) respiratory power ($P_{i,r}$), which moves air in and out of the lungs, and (3) heart power ($P_{i,h}$), which pumps blood. Thus the total power (P_i) required for flight in a horizontal airstream at constant altitude is the sum

$$P_i = (P_{o,in} + P_{o,par} + P_{o,pr})/E + P_{i,B} + P_{i,r} + P_{i,h} \quad (1)$$

where E is the efficiency of the flight muscles.

EFFECT OF ALTITUDE AND TEMPERATURE

Each of the terms in equation (1) has been analyzed separately (Pennycuik, 1968; 1969; Tucker, 1973), either for birds flying at sea level, or through air with different densities. Some of the terms are influenced by air viscosity as well. When appropriate terms are expressed as functions of both viscosity (μ) and density (ρ), equation (1) is applicable to flight at different altitudes and temperatures, since density and viscosity themselves are functions of altitude and temperature. The analysis of these terms, which can be found in the Appendix, leads to the following equation for level flight.

$$P_i = 1.11 \left[(2(mg)^2 / (0.7\pi\rho b^2 V) + 434(\rho\mu)^{1/2} A_o V^{5/2}) \left(1 + 471 \left(\frac{\mu}{\rho m^{1/3} V} \right)^{1/2} \right) / E + P_{i,B} \right] \quad (2)$$

The quantities to which the symbols refer are given in Table 1.

Equation (2) can be solved after assigning ρ and μ values to represent the altitude and temperature combination of choice. Tables or equations that describe the United States standard atmosphere give ρ , μ and temperature at different altitudes (see Appendix), and I will use the U.S. standard atmosphere (Table 2) in subsequent calculations of altitude effects.

The power requirement calculated from equation (2) is in watts, the SI unit for power. If A_o , the equivalent flat plate area, is not measured, it can be approximated in m^2 by the equation

$$A_o = 0.00334m^{0.66} \quad (3)$$

where m is body mass in kg. Likewise, the wingspan (b) is approximated in meters by

$$b = 1.1m^{1/3} \quad (4)$$

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TABLE 1

SYMBOLS

a	regression coefficient	S	area
A	equivalent flat plate area	t	time
b	wing span	T	absolute temperature
c	regression coefficient	U	ground speed
C _D	drag coefficient	μ	air viscosity
E	muscle efficiency	V	air speed
E'	partial efficiency	V'	air speed for minimum cost of transport over ground
f	a function	W	wind speed
F	force	w	body weight
g	acceleration of gravity (9.81 m/sec ²)	x	distance
h	altitude	y	distance
k	constant	α	angular horizontal flight heading, relative to hori- zontal wind direction.
ℓ	length	θ	angle of flight direction relative to horizontal
m	mass	φ	angle between flight direc- tion and magnitude of weight for polar coordi- nates.
P	power for level flight relative to air		
P'	power for ascending, descending or level flight relative to air		
ρ	air density		
(Re)	Reynolds number		

SUBSCRIPT SYMBOLS

B	basal	min	minimum P _i
h	heart	n	an integer
hor	horizontal	o	output
i	input	par	parasite
in	induced	pr	profile
I	an integer	tun	tunnel
m	mask plus tube	vert	vertical

Basal metabolic rate (P_{i,B}) is approximated in watts by

$$P_{i,B} = 6.15m^{0.724} \tag{5}$$

for passerines, and

$$P_{i,B} = 3.73m^{0.723} \tag{6}$$

for nonpasserines. These equations are justified in Tucker (1973). All of the birds that are discussed in this paper have characteristics that are given by equations (3), (4) and (5).

TABLE 2

Air density (ρ), viscosity (μ) and temperature (T) at different altitudes (h) for the United States standard atmosphere.

h (m)	ρ (kg/m ³)	μ (kg/ (m sec))	T (K)
0	1.225	17.8×10^{-6}	288
1500	1.058	17.3×10^{-6}	278
3000	0.909	16.8×10^{-6}	269
4500	0.776	16.3×10^{-6}	259
6000	0.659	15.8×10^{-6}	249

APPROXIMATION EQUATIONS

Since equation (2) is tedious to solve without the aid of a computer, it is useful to generate simpler equations that yield approximately the same answers under certain conditions, and can be solved quickly with a slide rule. The conditions are: (1) the bird has a body mass (m) between 0.003 kg and 10 kg, and flies at an altitude (h) between 0 and 6000 m in the U.S. standard atmosphere, (2) the bird flies at constant airspeed and altitude, (3) there is no wind, (4) the bird's equivalent flat plate area, wingspan, and basic metabolic rate are given by equations (3), (4), and (5), respectively.

If the bird flies at an airspeed V such that "cost of transport through the air" (see section on horizontal air movements, below) is minimum, then approximately,

$$V = (835.3 \times 10^{-6}h + 15.73)m^{0.169} \quad (7)$$

This equation yields values for V that are within 5% of those calculated from equation (2).

The power required to fly at the airspeed for minimum cost of transport through the air is given approximately by

$$P_i = (6.43 \times 10^{-3}h + 94.15)m^{0.974} \quad (8)$$

This equation yields values that are within 16% of those calculated from equation (2).

If the bird's wingspan is appreciably different from the value predicted by equation (4) for its body mass, both V and P_i are affected. For birds with wingspans only 0.8 times the value calculated from equation (4), approximately

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$$V = (954.7 \times 10^{-6}h + 17.66)m^{0.169} \quad (9)$$

$$P_i = (8.60 \times 10^{-3}h + 122.9)m^{0.974} \quad (10)$$

For birds with wingspans 1.2 times the value calculated from equation (4), approximately

$$V = (760.7 \times 10^{-6}h + 14.28)m^{0.169} \quad (11)$$

$$P_i = (5.09 \times 10^{-3}h + 76.21)m^{0.974} \quad (12)$$

The derivation of these approximation equations is given in the Appendix.

EFFECT OF WIND VELOCITY

VERTICAL AIR MOVEMENTS

The air through which a bird flies may have both vertical velocity components (W_{vert}) and horizontal components (W_{hor}) relative to the earth. The magnitude of the vertical components have a large influence on the power requirements of a bird flying at constant altitude. If the bird flies in an up-draft ($W_{\text{vert}} > 0$) then less power is required than if the bird flies in a down-draft ($W_{\text{vert}} < 0$). The change in power required to maintain altitude in an up- or down-draft is given by

$$\Delta P_i = -wW_{\text{vert}}/E' \quad (13)$$

where E' is partial efficiency and w is body weight in newtons. Partial efficiency is near 0.25 in the birds for which it has been measured (Tucker, 1972; Bernstein, et al., 1973). The definition of partial efficiency and the derivation of equation (13) are given in the Appendix. Thus,

$$P'_i = P_i + \Delta P_i \quad (14)$$

where the two terms on the right are given by equations (2) and (13). This equation gives the power requirements for flight at various constant altitudes, and in air with various vertical velocity components. For example, the power requirement for flight in still air at constant altitude (sea level) and at an airspeed of 11m/sec by a bird with a mass of 0.125 kg is 11.5 watts. A vertical wind component of 1m/sec, which is not unusual, changes the power requirement by 43%.

HORIZONTAL AIR MOVEMENTS

When a bird flies at some airspeed at constant altitude in a wind with a constant horizontal velocity component, the airflow around the bird is independent of the horizontal wind velocity. In other words, the power required to fly through the air is the same whether the air is moving horizontally relative to the earth or not, i.e., whether the bird flies in a head-, side- or tailwind. However, birds are concerned

not merely with moving through the air but with moving from one point on the earth to another. The power required to fly at some particular groundspeed (rather than airspeed) is greatly influenced by the horizontal velocity of the wind.

The influence of horizontal winds on the energetic cost of moving from one point on the surface of the earth to another at the same altitude can be measured by calculating the quantity "energy used per distance traveled over the ground." If the differential dx is some small distance traveled over the ground, then de is approximately the amount of energy required to move this distance. Thus, since $P'_i = de/dt$ and ground speed (U) is dx/dt , the instantaneous value (de/dx) of the quantity "energy used per distance traveled over the ground" is given by the ratio P'_i/U , where U is the magnitude of the vector sum of the horizontal components of air velocity and wind velocity. Furthermore, it is convenient to calculate this ratio per unit body weight. Then, the "cost of transport over the ground" is given by the dimensionless number $P'_i/(wU)$.

Likewise, the "cost of transport through the air" at constant altitude is given by $P'_i/(wV)$. Clearly, when windspeed is zero, $P'_i/(wV) = P'_i/(wU)$, i.e., the cost of transport through the air and the cost of transport over the ground are equal.

The cost of transport through the air for a bird of a particular weight flying under given conditions is obtained by dividing equation (14) by wV . Typically, the cost of transport has a minimal value at a particular airspeed towards the high end of the bird's range of airspeeds. It increases rapidly as speed decreases and less rapidly as speed increases (Fig. 1). It is evident that a bird can travel a given distance through the air with the least energy expenditure if it flies at the speed where the cost of transport through the air is minimal.

The cost of transport over the ground is obtained by dividing equation (14) by wU , and also has a minimum value at some particular airspeed. Thus, a bird can cover distance over the ground with the least energy expenditure if it flies at the airspeed such that the cost of transport over the ground is minimal.

FLIGHT RANGE

The minimum cost of transport over the ground is a useful quantity with which to describe birds, for it allows one to calculate the maximum distance that a bird can fly on a given amount of fuel. This is a particularly interesting calculation for those birds that make long migratory flights over seas or deserts where they cannot stop en route to feed. The calculation is a complex one, for it must account for the fact that body mass decreases during the flight as fuel is used up. Consequently, the speed for minimum cost of transport decreases, and so do the power requirements for flight (Fig. 2). Happily, the results are simple to describe when certain assumptions are made. These are: (1) that the wind velocity is constant over the flight path, (2) that the

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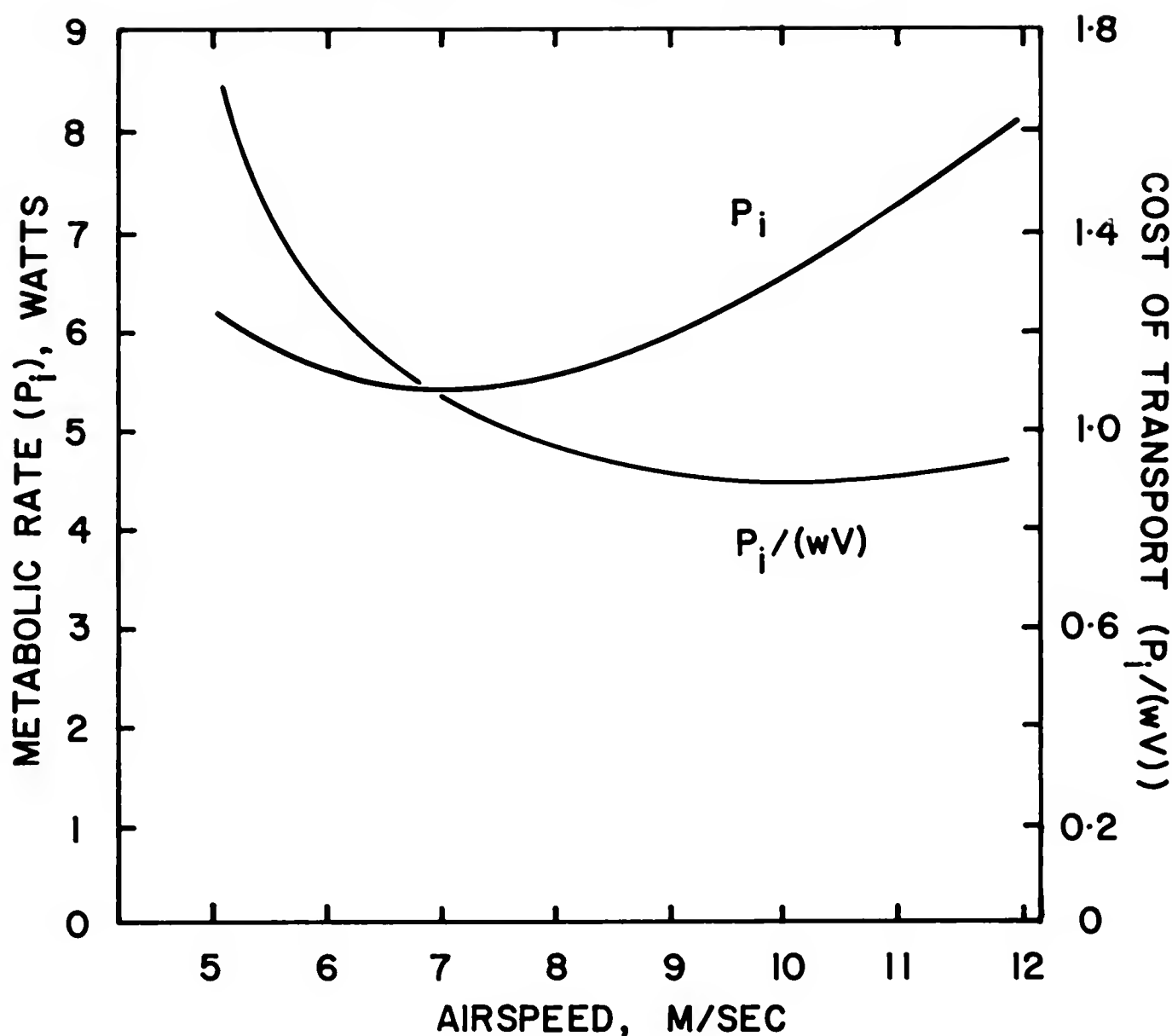


FIG. 1. Theoretical metabolic rate (P_i) and cost of transport through the air ($P_i/(wV)$) for a bird with a mass of 0.075 kg flying horizontally at various speeds at sea level through still air.

bird flies at a constant altitude, air temperature, and heading relative to the horizontal wind component, and (3) that it flies long enough to use up 20% of its preflight weight as fuel (fat). Under these conditions the minimum cost of transport over the ground varies less than 10% throughout the flight for altitudes below 6,000 m and reasonable winds (not exceeding 5 m/sec in horizontal speed and 1 m/sec in vertical speed). (See Appendix for supporting calculations.)

The virtual constancy of the minimum $P'_i/(wU)$ value throughout the flight under the above conditions makes the range of a bird easy to calculate. We can assume that a bird on a long distance flight uses fat as fuel and is in water balance (Tucker, 1971). Thus,

$$dm/dt = -k_1 P'_i \quad (15)$$

where $k_1 = 2.56 \times 10^{-8}$ kg fat/joule. Also

$$U = dx/dt \quad (16)$$

where x = distance travelled over the ground. Considering the cost of transport to be constant

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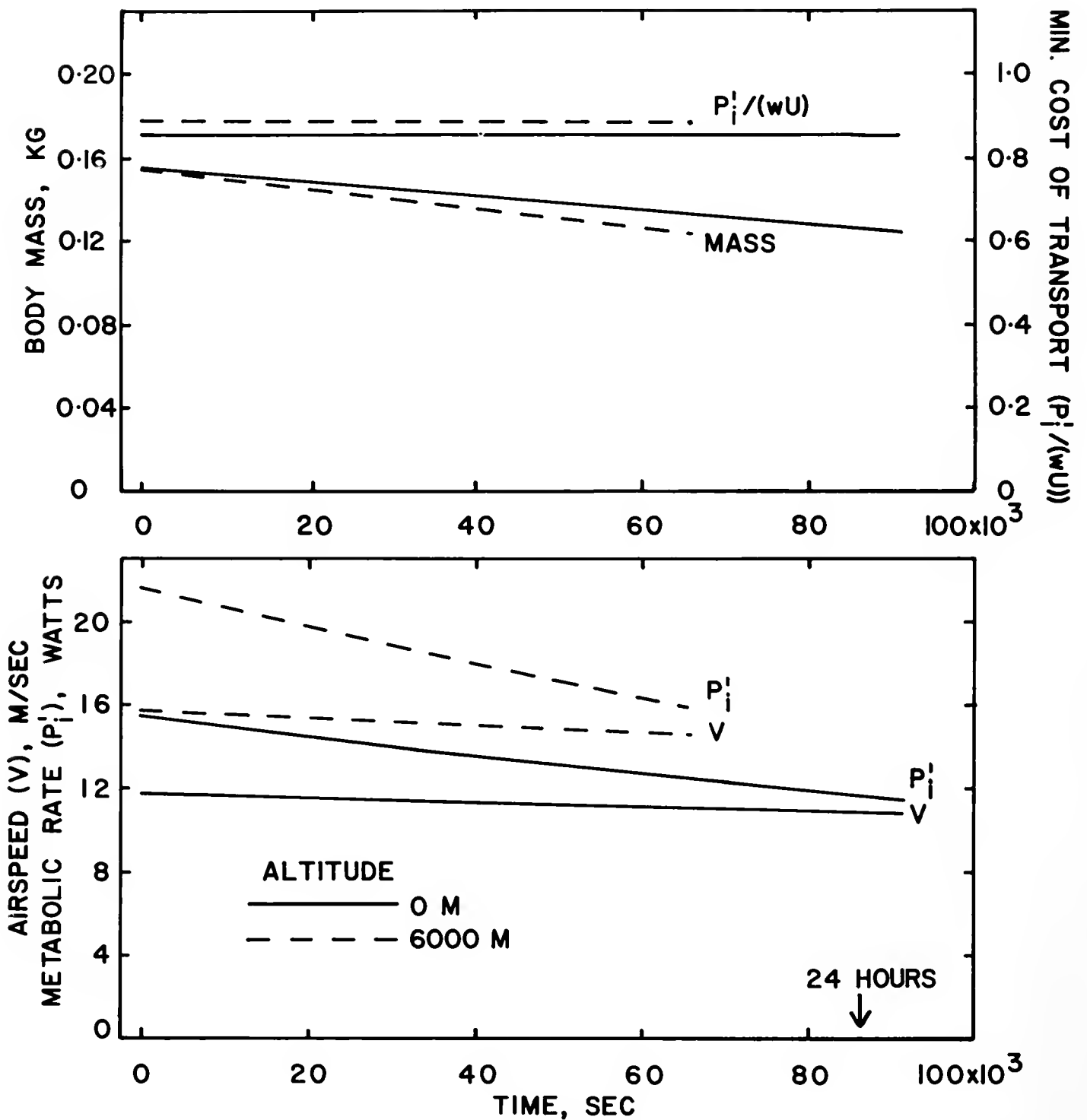


FIG. 2. Changes at two altitudes in body mass (m), minimum cost of transport over the ground (P'_i/wU), speed for minimum cost of transport (V) and metabolic rate (P'_i) for minimum cost of transport during a flight in which 20% of the initial body mass is consumed as fuel (fat). Full lines are for a flight at sea level, broken lines for a flight at an altitude of 6,000 m. The bird has an initial body mass of 0.156 kg and wind velocity is 0. The bird covers a total distance of 1,040 km at sea level, and 996 km at 6,000 m.

$$P'_i/(wU) = k_2 \quad (17)$$

and substituting equations (15), (16) and the relation $w = mg$, yields

$$dx = \frac{-dm}{k_1 k_2 mg} \quad (18)$$

Integrating yields the equation

$$x = \frac{\ln(m_0/m_1)}{k_1 k_2 g} = \frac{\log_{10}(m_0/m_1)}{1.09 \times 10^{-7} k_2} \quad (19)$$

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where x is the distance travelled by a bird whose initial mass is m_0 and final mass is m_1 . The value of k_2 can be quickly calculated at sea level when the wind velocity is zero from the empirical equation

$$P'_i/(wU) = k_2 = 0.896w^{-0.227} \tag{20}$$

(Tucker, 1970; 1973), where w is weight in newtons. For other conditions the equations given by the theory in this paper must be evaluated.

Examples of how the minimum cost of transport over the ground and the associated airspeeds vary for two different wind velocities and altitudes are shown for a bird with a mass of 0.125 kg in Figures 3 and 4. There is either no wind or else it is blowing at 5 m/sec in the indicated direction and has no vertical velocity component. A line

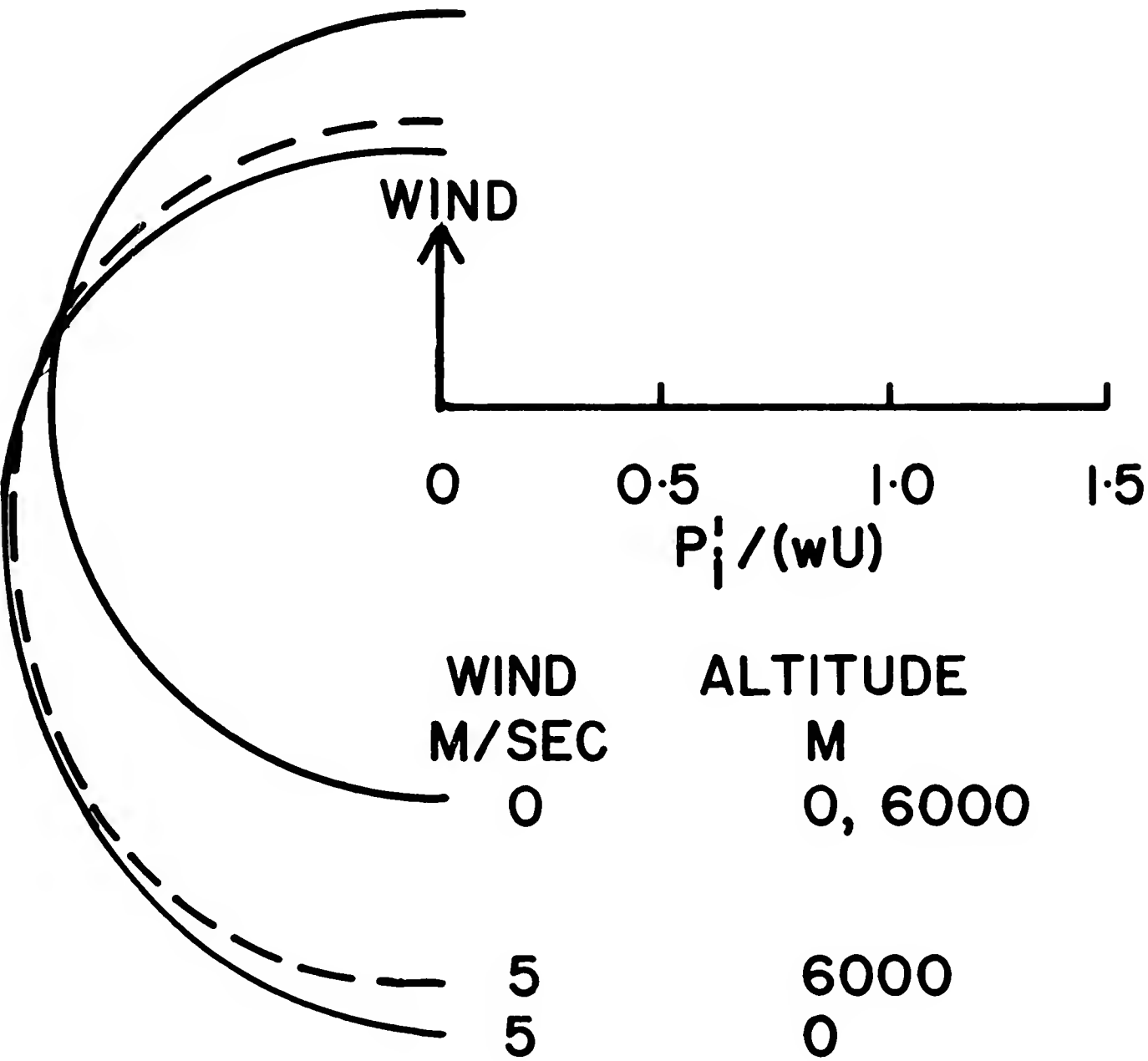


FIG. 3. Minimum costs of transport over the ground ($P'_i/(wU)$) at two altitudes in no wind or in a horizontal wind with a horizontal speed of 5 m/sec and no vertical component. The semicircle drawn with a full line describes minimum cost of transport in no wind at both sea level and an altitude of 6,000 m, since the two curves superimpose. The other curves describe flight in a wind of 5 m/sec at sea level (full line) or at 6,000 m (broken line). The wind direction is shown by an arrow, and the direction of a line connecting a point on the curve to the base of the arrow is the direction that the bird flies relative to the wind to achieve the indicated cost of transport. The bird has a mass of 0.125 kg.

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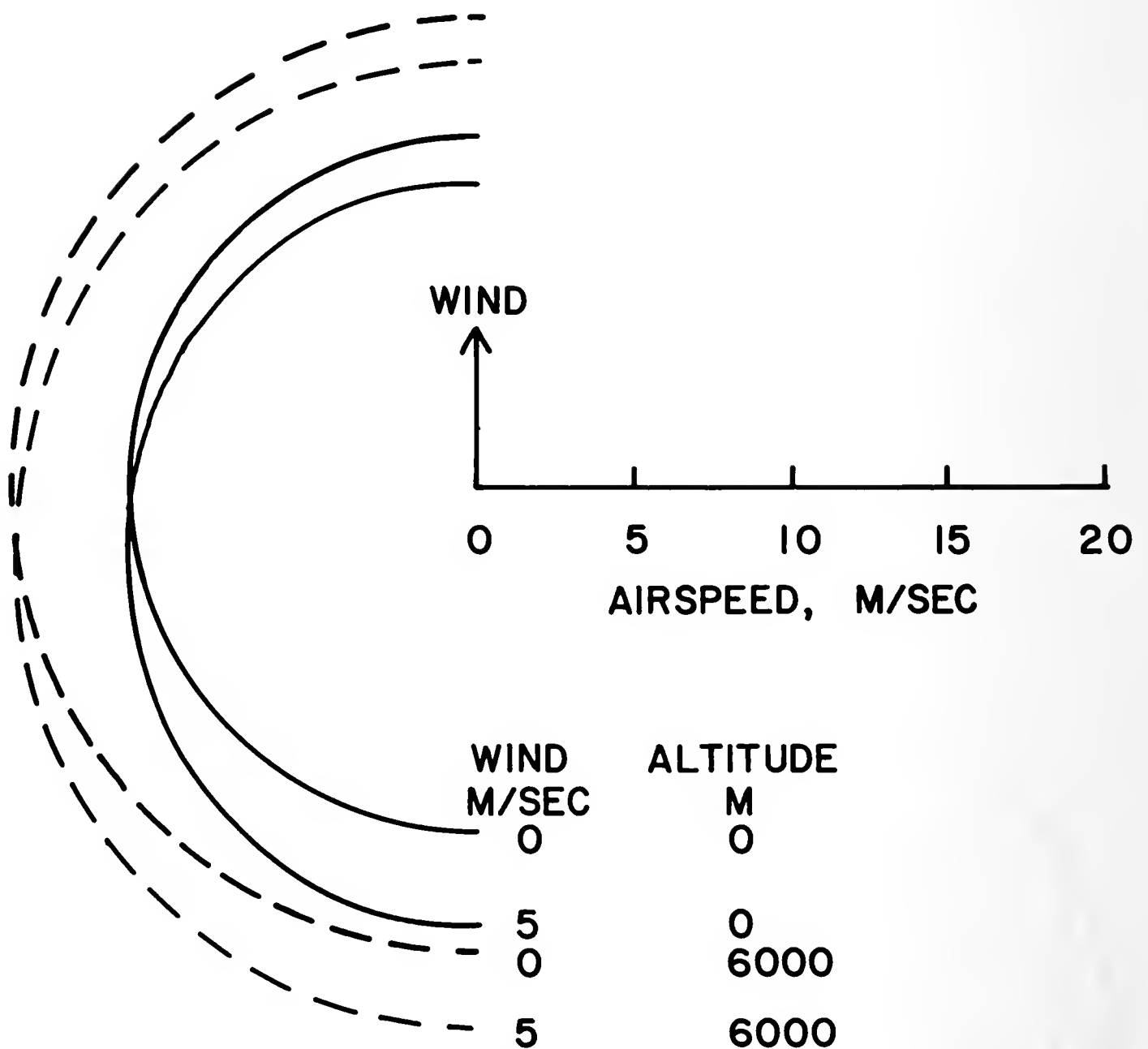


FIG. 4. Air speeds at two altitudes for minimum costs of transport over the ground in no wind or in a wind with a horizontal speed of 5 m/sec and no vertical component. The full lines are for flight at sea level and the broken lines are for flight at an altitude of 6,000 m. The wind direction is shown by the arrow and a line connecting a point on a curve to the base of the arrow indicates the direction of the bird's flight path over the ground. The bird has a mass of 0.125 kg.

between the origin and any point on the curve indicates the direction of the flight path over the ground for the airspeed or cost of transport corresponding to the intersection of the line and the curve.

There are several features of Figures 3 and 4 that give interesting quantitative information for a 0.125 kg bird flying in the specified conditions, and qualitative information for birds of other sizes flying in other conditions. In still air, the minimum cost of transport is nearly independent of altitude. However, in a given wind, minimum cost of transport over the ground increases with altitude for a bird flying down-wind but decreases with altitude for a bird flying up-wind. These changes are not large, amounting to less than a 15% difference in cost of transport between an altitude of zero and 6,000 m for up-wind and down-wind flight in Figure 3. Of course, a wind of 5 m/sec has a large influence on minimum cost of transport over the ground since

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the bird's airspeed is between 10 and 17 m/sec. For example, the bird in Figure 3 has a 64% increase in minimum cost of transport over the ground at sea level when flying into a 5 m/sec headwind compared to still air. On the other hand, its minimum cost of transport over the ground is reduced 33% at sea level when flying with a 5 m/sec tailwind compared to still air. Since cost of transport over the ground is inversely proportional to range [equation (19)], a bird with an initial mass of 0.125 kg that has enough fuel to fly 1,000 km in still air at sea level could fly 1,500 km with a 5 m/sec tailwind, but only 610 km with a 5 m/sec headwind. Wind speeds of 5 m/sec are common during the migrating season (Visser, 1954), and they obviously have a large influence upon the energetic cost of covering distance over the ground.

Figure 4 shows the initial airspeeds of a 0.125 kg bird that has the minimum costs of transport over the ground shown in Figure 3. At both sea level and altitudes of 6,000 m, it is beneficial from an energetic point of view to fly faster into a headwind, and slower with a tailwind than is the case in still air. Such behavior has been observed in birds (Bruderer, 1971; Tucker and Schmidt-Koenig, 1971). Airspeed for minimum cost of transport always increases with altitude.

The top altitude of 6,000 m (19,700 ft) in Figures 3 and 4 is an extreme one for birds, although some birds fly this high (Tucker, 1968; Hilditch, et al., 1973). For wind velocities that do not change with altitude, there seems to be only a trivial energetic advantage for high altitude rather than sea level flight in a headwind, and also a trivial disadvantage in a tailwind. However, winds commonly increase their velocity by a factor of 2 between sea level and altitudes of a few thousand meters, and change their directions as well. Thus a bird could often greatly increase its range by flying at high altitudes with a tailwind, but doing so with a headwind could be an energetic disaster.

How do the distances that birds are known to fly in nature on a given amount of fuel compare with the predictions of the theory? The predictions from the equations given here for distances flown through the air (assuming no vertical wind velocity components) are essentially the same as those calculated by Tucker (1971) for birds of various sizes (Fig. 5). Some birds fly as far or further over the ground than the upper margin of the zone shown in Figure 5 indicates. For example, hummingbirds with a mass of 5×10^{-3} kg fly over 800 km (500 miles) across the Gulf of Mexico (Lasiewski, 1962), Blackpoll Warblers (*Dendroica striata*) with a mass of 20×10^{-3} kg fly 1,300 km (800 miles) from New England to Bermuda, and perhaps an additional 1,300 km to the West Indies (Nisbet, et al., 1963), and Golden Plovers (*Pluvialis dominica*) with a mass of 0.2 kg fly 3,900 km (2,400 miles) from the Aleutian to the Hawaiian Islands (Johnston and McFarlane, 1967).

A flight range over the ground that is greater than flight range through the air is consistent with the theory only if the bird is flying

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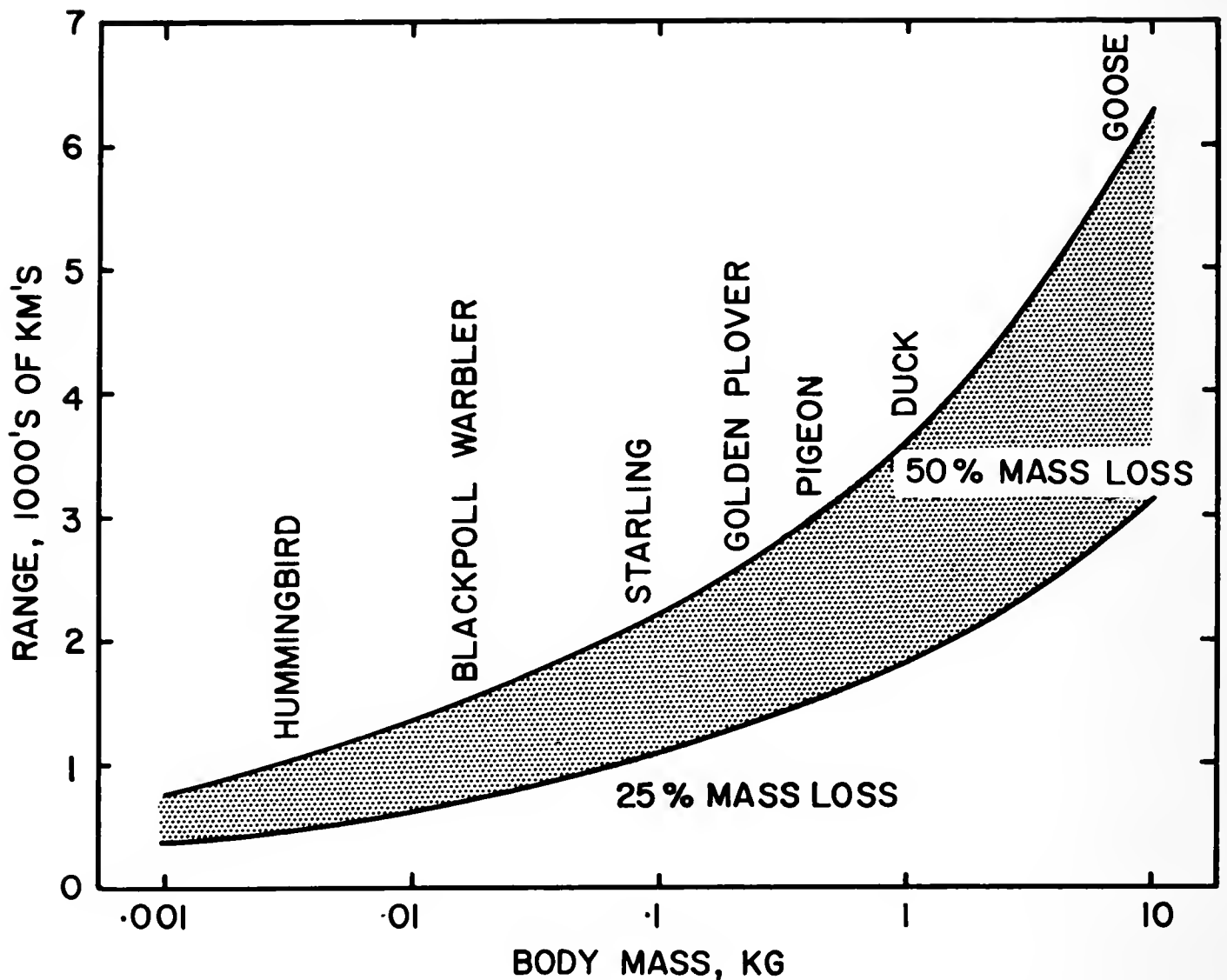


FIG. 5. Flight range through the air of birds with various body masses when fat is the fuel for flight. Some birds are named as examples of different masses. Curves are shown for two different amounts of fuel consumed, expressed as a proportion of initial body mass. A fuel consumption of 25% of body mass is a reasonable estimate for long-distance migrants and 50% body mass consumption appears to be a maximum limit. From Tucker, 1971.

in a wind with either tailwind components or up-drafts. It seems unlikely that the predictions of the theory could be wrong by more than 50%, yet some long-distance, non-stop flights would indicate nearly this magnitude of error if one assumed that the birds were flying in still air, and would indicate a much larger error if the birds were hindered by headwinds or down-drafts. The available evidence suggests that the longest, non-stop flights of birds are physiologically possible only if the birds are aided, or at least not hindered, by the wind. Field observations support this view (Able, 1973).

APPENDIX

COMPONENTS OF BODY WEIGHT AND ASSOCIATED PARASITE POWER

Body weight force components ($F_{w,x}$) parallel to the direction of flight (Fig. 6).

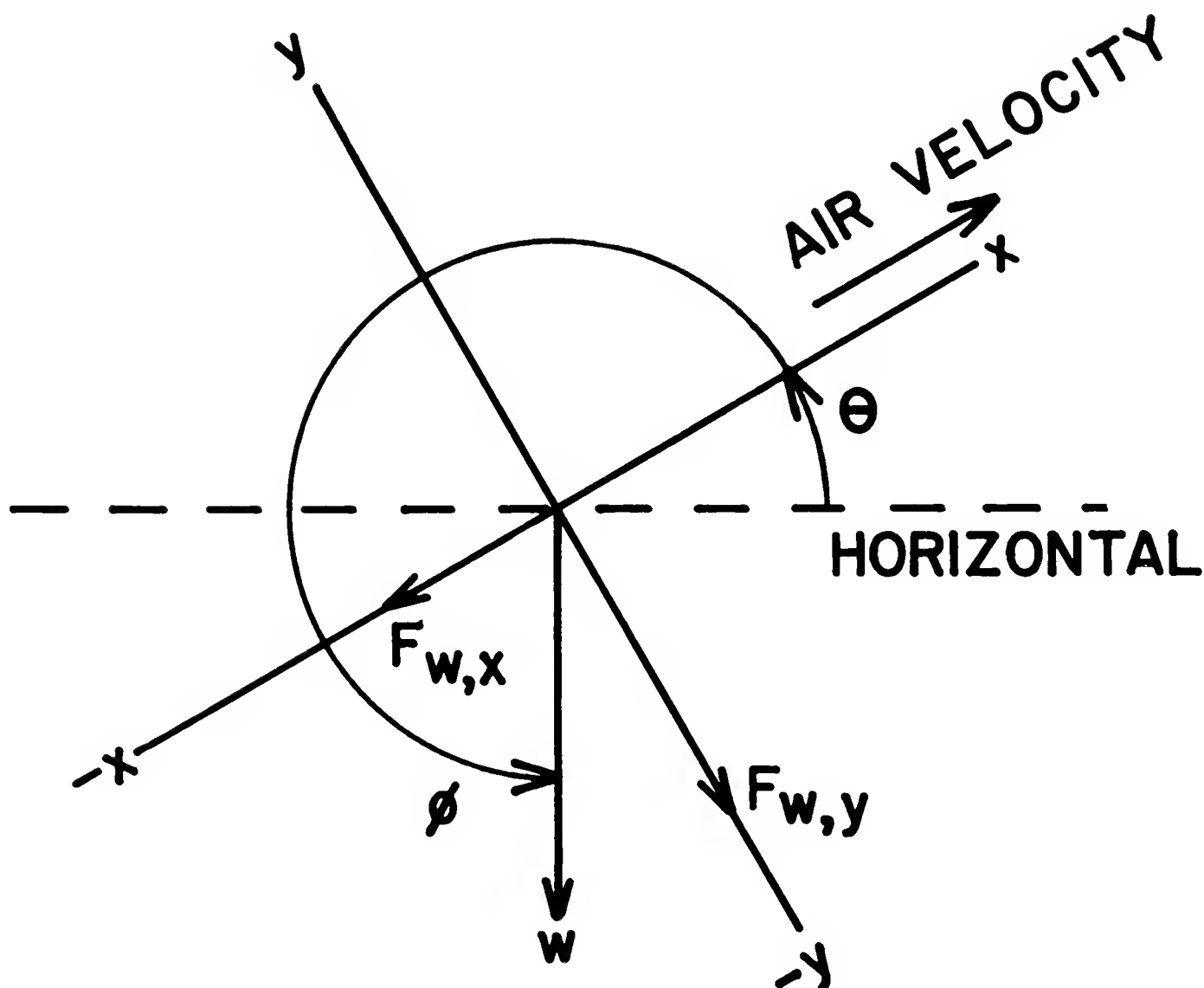


FIG. 6. Body weight force components parallel to ($F_{w,x}$) and perpendicular to ($F_{w,y}$) the flight direction relative to the air. This diagram corresponds to a bird flying to the right through still air and climbing at angle θ .

$$F_{w,x} = w \cos \phi \quad (21)$$

since

$$\phi = 270^\circ - \theta \quad (22)$$

$$F_{w,x} = w \cos (270^\circ - \theta) = -w \sin \theta \quad (23)$$

Body weight force components ($F_{w,y}$) perpendicular to the direction of flight (Fig. 6).

$$F_{w,y} = w \sin \phi = -w \cos \theta \simeq -w \text{ for } \theta \text{ small} \quad (24)$$

Parasite power.

The parasite power expenditure ($P_{o,par}$) to move the body (exclusive of the wings) through the air at air speed V (relative to the air) is

$$P_{o,par} = -FV \quad (25)$$

where F is the force component on the body parallel to the x-axis.

At constant speed,

$$\Delta P_{o,par} = -V\Delta F \quad (26)$$

where $\Delta F = F_2 - F_1$ and $\Delta P_{o,par} = P_{o,par,2} - P_{o,par,1}$

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PARTIAL EFFICIENCY (E')

By definition,

$$E' = \frac{\Delta P_{o,par}}{\Delta P_i} \quad (27)$$

where ΔP_i is the change in metabolic rate of the bird that accompanies $\Delta P_{o,par}$.

If the bird flying at constant speed changes its flight angle from θ_1 to θ_2 , then $\Delta \sin \theta = \sin \theta_2 - \sin \theta_1$, and

$$\Delta F = -w \Delta \sin \theta \quad (28)$$

Therefore, from equations (26) and (28)

$$\Delta P_{o,par} = Vw \Delta \sin \theta \quad (29)$$

and

$$E' = \frac{Vw \Delta \sin \theta}{\Delta P'_{i,m}} \quad (30)$$

where $\Delta P'_{i,m}$ is the change in metabolic rate of a masked bird flying in the wind tunnel at constant speed, as the tunnel is tipped from θ_1 to θ_2 . E' typically has values between 0.2 and 0.3, for θ between $\pm 5^\circ$ and is assumed to be constant in the following discussion.

CORRECTION FOR AERODYNAMIC DRAG OF MASK AND TUBE

When a mask and tube are attached to a bird flying at $\theta = 0$ and speed V , from equation (26), the bird's power output to overcome the increased parasite drag changes by

$$\Delta P_{o,par} = -V\Delta F_m$$

where F_m is the drag force added by the mask and tube. This force can be measured directly with a flight balance (see Tucker, 1972, for details).

From equation (27), the corresponding change in power input is

$$\Delta P_{i,m} = \frac{\Delta P_{o,par}}{E'}$$

where $\Delta P_{i,m}$ is the difference between the power inputs of the bird before (P_i) and after ($P_{i,m}$) the drag of the mask and tube has been added. Thus, $P_i = P_{i,m} - \Delta P_{i,m}$.

CORRECTION FOR PITCHING MOMENT DUE TO MASK AND TUBE WEIGHT

Figure 7 shows the added weight of the mask and tube (Δw), the increased vertical force of the tail (ΔF_{vert}) to counteract the mask and tube weight, and the increased drag on the tail (ΔF_{hor}) required to

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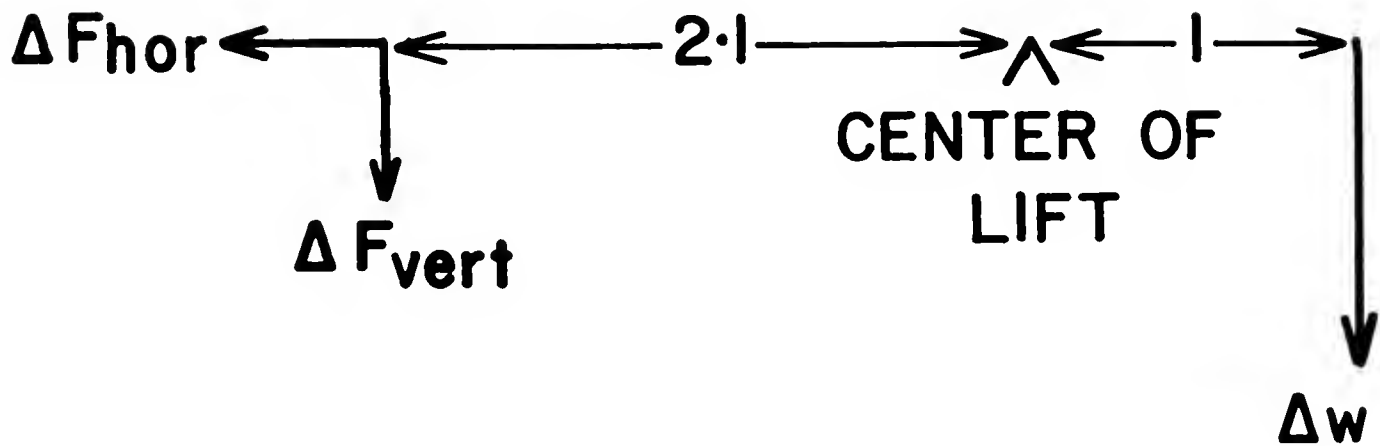


FIG. 7. Force components (ΔF_{hor} , ΔF_{vert}) exerted by the tail to compensate for the pitching moment due to the weight of the mask and tube (Δw). This diagram corresponds to a bird flying level and to the right.

produce ΔF_{vert} . The moment arms for F_m and F_{vert} are l and $2l$ respectively. Since the mask and tube together comprise about 4% of total body weight (w)

$$\Delta w = 0.04 w \quad (31)$$

I assume that the ratio of $\Delta F_{vert}/F_{hor}$ is 1, which is a reasonable value for objects shaped like tails. When the pitching moments balance

$$2l \Delta F_{vert} = -l \Delta w \quad (32)$$

and

$$\Delta F_{vert} = -0.02 w \quad (33)$$

Therefore,

$$\Delta F_{hor} = -0.02 w \quad (34)$$

Since, from equation (26)

$$\begin{aligned} \Delta P_{o,par} &= -V \Delta F_{hor}, \\ \Delta P_i &= \frac{V \times 0.02 w}{E'} \end{aligned} \quad (35)$$

where ΔP_i is the increase in power input required to compensate for the pitching moment due to the mask and tube. Values of ΔP_i calculated for Budgerigars and gulls at various speeds are less than 0.2% of P_i .

EFFECTS OF VERTICAL AIR MOVEMENTS

The diagram (Fig. 8) shows the components of a bird's velocity vector (\bar{V}) relative to air when flying at constant altitude in an updraft, i.e., the wind velocity has a vertical component (W_{vert}) directed upwards.

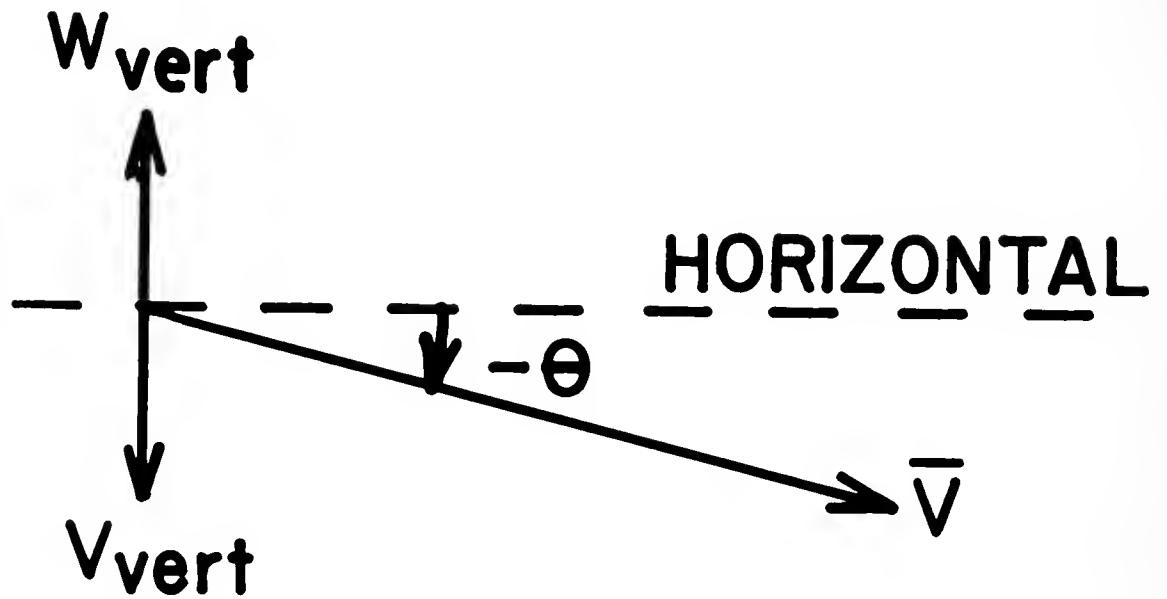


FIG. 8. Air velocity vector (\bar{V} , relative to air) and its vertical component (V_{vert}) for a bird flying to the right at constant altitude in wind with a vertical velocity component W_{vert} (relative to earth).

It is clear that

$$\sin \theta = V_{\text{vert}}/V \quad (36)$$

and that

$$\Delta \sin \theta = V_{\text{vert}}/V \quad (37)$$

when $\sin \theta_1 = 0$ —i.e., flight in wind with no vertical velocity component. Since, from equation (28)

$$\Delta F = -w \Delta \sin \theta = \frac{-w V_{\text{vert}}}{V} \quad (38)$$

then

$$\Delta P_{o,\text{par}} = w V_{\text{vert}} \quad (39)$$

Thus

$$\Delta P_i = \frac{\Delta P_o}{E'} = \frac{w V_{\text{vert}}}{E'} \quad (40)$$

or

$$\Delta P_i = \frac{-w W_{\text{vert}}}{E'} \quad (41)$$

where $\Delta P_i = P_i' - P_i$, P_i' is the power input required to fly at any θ between approximately $\pm 5^\circ$ and P_i is the power required to fly at $\theta = 0$.

METABOLIC RATE (P_i) FOR ZERO PROFILE DRAG AND A MUSCLE EFFICIENCY OF 0.3

The theory that describes the metabolic rates of birds flying level in the wind tunnel is represented by the equation

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$$P_{i,tun} = 1.11[(P_{o,in} + P_{o,par})(1 + F_{tun}m^{-1/6}V^{-1/2})/E_{tun} + P_{i,B}] \quad (42)$$

(Tucker, 1973) where the quantities are identified in Table 1 and the subscript "tun" indicates values for experiments in the wind tunnel. A similar equation could be written where each "tun" subscript is replaced with "min", indicating values for the subscripted variables on the right side of the equation chosen so as to minimize $P_{i,min}$. Then

$$\frac{P_{i,min}}{P_{i,tun}} \simeq \frac{(1 + F_{min}m^{-1/6}V^{-1/2})/E_{min}}{(1 + F_{tun}m^{-1/6}V^{-1/2})/E_{tun}} \quad (43)$$

where the basal metabolic rate ($P_{i,B}$) has been taken as 0. This approximation does not result in significant errors for our present purposes.

Now $P_{i,min}$ can be obtained by choosing the maximum value of muscle efficiency (E) and assuming that profile power is 0. The latter is achieved by setting F_{min} equal to 0, and the maximum possible muscle efficiency is given by $E_{min} = 0.3$. Since $E_{tun} = 0.2$ and $F_{tun} = 1.8$

$$\frac{P_{i,min}}{P_{i,tun}} = \frac{0.667}{1 + 1.8m^{-1/6}V^{-1/2}} \quad (44)$$

As examples, consider two birds flying at a speed of 12 m/sec, one with a body mass of 0.03 kg, the other with a mass of 0.3 kg. For the smaller bird,

$$\frac{P_{i,min}}{P_{i,tun}} = 0.35 \quad (45)$$

and for the larger bird,

$$\frac{P_{i,min}}{P_{i,tun}} = 0.41 \quad (46)$$

That is, the metabolic rates ($P_{i,min}$) of these birds would be only one-third to two-fifths of those ($P_{i,tun}$) they would have in the wind tunnel.

CORRECTION FOR THE WEIGHT OF THE MASK AND TUBE

When a bird carries the excess weight (Δw) of a mask and tube, its metabolic rate (P_i) increases. The approximate value of ΔP_i for a given Δw can be calculated. In the previous section, the metabolic rate of a bird flying level in a wind tunnel was given by

$$P_i = 1.11[(P_{o,in} + P_{o,par})(1 + 1.8m^{-1/6}V^{-1/2})/E + P_{i,B}] \quad (47)$$

where

$$P_{o,in} = \frac{2w^2}{0.7\pi\rho b^2V} \quad (48)$$

(Tucker, 1973) (see Table 1 for symbols). The variable w (total body

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weight) is the only variable in equation (47) that will change due to the addition of the weight of the mask and tube. The change in P_i due to the addition of this weight is given approximately by

$$\Delta P_i \simeq \frac{dP_i}{dw} \Delta w \quad (49)$$

where, after substituting the expression for $P_{o,in}$,

$$\frac{dP_i}{dw} = \frac{4.44 w (1 + 1.8m^{-1/6}V^{-1/2})}{0.7\pi\rho b^2VE} \quad (50)$$

For example, consider a Laughing Gull with a mass of 0.322 kg flying level at $V = 12$ m/sec. The bird's wingspan (b) is 0.93 meters, air density (ρ) is 1.18 kg/m³, the acceleration due to gravity (g) is 9.81 m/sec², and the muscular efficiency (E) is 0.2. The added mass of the mask and tube is 10.4×10^{-3} kg, so that $\Delta w = 0.102$ newtons. These values yield

$$\frac{dP_i}{dw} = 4.24 \text{ watts/newton}$$

and

$$\Delta P_i \simeq 0.432 \text{ watts.}$$

This value for ΔP_i is 2.2% of the value for P_i calculated from the first equation in this section.

The ΔP_i value for a Budgerigar is 3.1% of the calculated value for P_i . The Budgerigar has a mass of 0.035 kg, a wingspan of 0.235 meters, and carries a mask and tube with a mass of 1.48×10^{-3} kg. All other variables have the same values as in the previous example.

INFLUENCE OF AIR DENSITY AND VISCOSITY ON THE POWER REQUIRED FOR LEVEL FLIGHT

The total power required for level flight (P_i) is given by equation (1)

$$P_i = (P_{o,in} + P_{o,par} + P_{o,pr})/E + P_{i,B} + P_{i,r} + P_{i,h}$$

Induced power ($P_{o,in}$) supports the bird's weight and depends on air density (ρ) but not viscosity (μ). Thus, from equation (48)

$$P_{o,in} = 2(mg)^2/(0.7\pi\rho b^2V)$$

Parasite power ($P_{o,par}$) overcomes the drag of the bird's body exclusive of the wings and is given by

$$P_{o,par} = \rho S C_D V^3/2 \quad (51)$$

where S is some cross-sectional area of the bird's body and C_D is a drag coefficient. C_D is a function of Reynolds number (Re) (Tucker, 1973),

$$C_D \propto (Re)^{-1/2} \quad (52)$$

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where

$$(\text{Re}) = \frac{\rho l V}{\mu} \quad (53)$$

and l is some linear dimension of the bird's body. The equivalent flat plate area (A) of the bird's body is

$$A = SC_D \quad (54)$$

Therefore,

$$A \propto S \left(\frac{\rho l V}{\mu} \right)^{-1/2} \quad (55)$$

Thus, if A has the value A_o at ρ_o , μ_o , and V_o

$$\frac{A}{A_o} = \left(\frac{\rho V \mu_o}{\rho_o V_o \mu} \right)^{-1/2} \quad (56)$$

Combining equations (51), (54) and (56) yields

$$P_{o,\text{par}} = \frac{1}{2} \left(\frac{\rho \rho_o V_o \mu}{\mu_o} \right)^{1/2} A_o V^{5/2} \quad (57)$$

A_o , from measurements made in a wind tunnel at $V_o = 11$ m/sec is given by

$$A_o = 0.00334 \text{ m}^{0.66} \quad (58)$$

(Tucker, 1973). If ρ_o and μ_o are assigned the proper values for Durham where the experiments were done, then $\rho_o = 1.18$ kg/m³, $\mu_o = 1.72 \times 10^{-5}$ kg/(m sec) and

$$P_{o,\text{par}} = 434(\rho\mu)^{1/2} A_o V^{5/2} \quad (59)$$

Profile power ($P_{o,\text{pr}}$) is used in moving the wings and is difficult to measure (for example, see Pennycuik, 1968). However, the calculated power requirements for flight fit the wind tunnel measurements reasonably well if profile power is assumed to be given by

$$P_{o,\text{pr}} = f(\text{Re})(P_{o,\text{par}} + P_{o,\text{in}}) \quad (60)$$

where $f(\text{Re})$ is a function of (Re) given by

$$f(\text{Re}) \propto \text{Re}^{-1/2} \quad (61)$$

(Tucker, 1973). If l is some linear wing dimension, and

$$l \propto m^{1/3} \quad (62)$$

then

$$f(\text{Re}) = K \left(\frac{\rho m^{1/3} V}{\mu} \right)^{-1/2} \quad (63)$$

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The constant K is given by

$$K = f(Re_o) / \left(\frac{\rho_o m_o^{1/3} V_o}{\mu_o} \right)^{-1/2} \quad (64)$$

The calculated power requirements for flight agree with measurements reasonably well if

$$f(Re_o) / (m_o^{1/3} V_o)^{-1/2} = 1.8 \quad (65)$$

(Tucker, 1973). Combining equations (64) and (65) yields

$$K = 1.8 \left(\frac{\mu_o}{\rho_o} \right)^{-1/2} \quad (66)$$

After assigning ρ_o and μ_o the appropriate value for Durham, we get, from equations (60), (63) and (66)

$$P_{o,pr} = 471 \left(\frac{\mu}{\rho m^{1/3} V} \right)^{1/2} (P_{o,par} + P_{o,in}) \quad (67)$$

The remaining terms for basal metabolism ($P_{i,B}$), power for respiration ($P_{i,r}$) and power for circulation ($P_{i,h}$), and muscle efficiency (E) in equation (1) are assumed not to vary with ρ and μ . Since

$$P_{i,r} + P_{i,h} = 0.1 P_i \quad (68)$$

(Tucker, 1973)

$$P_i = 1.11 \left[(P_{o,in} + P_{o,par}) \left(1 + 471 \left(\frac{\mu}{\rho m^{1/3} V} \right)^{1/2} \right) / E + P_{i,B} \right] \quad (69)$$

Substituting equations (48) and (59) for $P_{o,in}$ and $P_{o,par}$ yields

$$P_i = 1.11 \left[(2(mg)^2 / (0.7 \pi \rho b^2 V) + 434(\rho \mu)^{1/2} A_o V^{5/2}) \left(1 + 471 \left(\frac{\mu}{\rho m^{1/3} V} \right)^{1/2} \right) / E + P_{i,B} \right] \quad (70)$$

STANDARD ATMOSPHERE

The power requirements of flight are influenced by both the density (μ) and viscosity (ρ) of the air, and these properties in turn depend upon air temperature (T) and atmospheric pressure. Pressure and temperature are influenced by altitude above the earth, although at a given altitude, they vary somewhat, according to the vagaries of the weather. The standard atmosphere has defined, unchanging values for density, viscosity, and temperature at each altitude, so that the flight characteristics specified for an aircraft at various altitudes in the standard atmosphere refer to known atmospheric conditions. In the United States the standard atmosphere up to an altitude (h) of 10,000

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m is described by the following equations (calculated from von Mises, 1959).

Absolute temperature, in kelvins, is given by

$$T = 288.0 - 6.5 \times 10^{-3} h \quad (71)$$

Density is related to both temperature and pressure, and in the standard atmosphere is given (in kg/m^3) by

$$\rho = 1.225(1 - 22.6 \times 10^{-6} h)^{4.256} \quad (72)$$

Viscosity is related to temperature but is nearly independent of pressure. At different temperatures, viscosity in $\text{kg}/(\text{m sec})$ is given by

$$\mu = \frac{2.705 \times 10^{-6} T^{3/2}}{1.8T + 223.2} \quad (73)$$

and in the standard atmosphere is given by

$$\mu = \frac{2.705 \times 10^{-6} (288 - 6.5 \times 10^{-3} h)^{3/2}}{741.6 - 11.7 \times 10^{-3} h} \quad (74)$$

APPROXIMATION EQUATIONS

I derived approximation equations by using linear least squares techniques to fit results calculated from the complete equations. The complete equations were solved under the following conditions: (1) the bird flies at constant altitude and at the constant airspeed where $P_i/(wV)$ is minimum, (2) there is no vertical wind component, (3) the bird's equivalent flat plate area, wingspan, and basal metabolic rate are given by equations (3), (4), and (5) respectively, and (4) density and viscosity are given at each altitude by equations (72) and (74), which describe the standard atmosphere.

Eight body masses ($m_1, m_2 \dots m_I, \dots m_8$) were chosen between 0.003 kg and 10 kg such that $m_I/m_{I-1} = 3.162$. The airspeed (V) at which $P_i/(wV)$ was minimum was calculated for each of these body masses at 5 altitudes ($h_1, h_2, \dots h_n, \dots h_5$) between 0 and 6000 m such that $h_n - h_{n-1} = 1500$ m. At each altitude, the relations between $\log V_I$ and $\log m_I$, and $\log P_{i,I}$ and $\log m_I$, were fitted with straight lines. Thus, I obtained the equations

$$V_n = a_{V,n} m^{c_{V,n}} \quad (75)$$

$$P_{i,n} = a_{P,n} m^{c_{P,n}} \quad (76)$$

for each of 5 altitudes, where a and c are the linear regression coefficients.

Next, I determined the relations between a , c , and altitude. The values of $c_{V,n}$ and $c_{P,n}$ were nearly constant (within 2% of the mean) for all altitudes, so c_V and c_P were assigned the mean values. I fitted the relations between $a_{V,n}$ and h_n , and $a_{P,n}$ and h_n , with straight lines to obtain

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$$a_v = k_1 h + k_2 \quad (77)$$

$$a_p = k_3 h + k_4 \quad (78)$$

where k_1, k_2, k_3, k_4 are the appropriate regression coefficients. Now, since

$$V = a_v m^{cv} \quad (79)$$

and

$$P_i = a_p m^{cp} \quad (80)$$

the approximation equations are obtained by substituting equations (77) and (78) into (79) and (80) to obtain

$$V = (k_1 h + k_2) m^{cv} \quad (81)$$

$$P_i = (k_3 h + k_4) m^{cp} \quad (82)$$

I repeated the process to obtain similar equations for V and P_i when wingspans were 0.8 and 1.2 times the values calculated from equation (4).

MINIMUM COST OF TRANSPORT OVER THE GROUND ($P'_i/(wU)$) AS BODY MASS CHANGES DURING FLIGHT

As a bird uses up fuel during a flight, its mass decreases. This decrease causes changes in every term of the equation that gives the power requirements for flight, except for basal metabolic rate, which is assumed to be constant. Thus, induced power decreases as body weight decreases, and parasite power decreases as the cross-sectional area of the body decreases. These changes are accompanied by a decrease in the speed at which cost of transport is minimum. The effect of all these changes on the minimum cost of transport over the ground ($P'_i/(wU)$) is complex to analyze, and only a general description of the analysis will be given here. The symbol "f" with a subscript indicates a functional relation between the variables accompanying it, and other variables that are not specified are taken to be constant.

For a bird of mass m flying at an airspeed of V and a groundspeed of U in a wind with vector velocity \bar{W}

$$P'_i = f_1(V, m) \quad (83)$$

The airspeed for maximum range over the ground (V') is achieved when P'_i/U is a minimum, and V' can be found by setting to 0 the partial derivative

$$\frac{\partial(P'_i/U)}{\partial V} = f_2(V', m) = 0 \quad (84)$$

Thus, solving for V' ,

$$V' = f_3(m) \quad (85)$$

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Now the rate of change of body mass relative to time (t) is proportional to the power requirements for flight

$$\frac{dm}{dt} = -k_1 P'_i = -k_1 f_1(V', m) \quad (86)$$

Substituting $f_3(m)$ for V' , and integrating yields

$$m = f_5(t) \quad (87)$$

Substituting equation (87) in equation (85) yields

$$V' = f_6(t) \quad (88)$$

Because dv'/dt is small, the amount of work involved in changing speed is so small that it need not be accounted for. Now equations (87) and (88) may be substituted into (83) to yield the P'_i value for minimum cost of transport

$$P'_i = f_7(t) \quad (89)$$

The bird's groundspeed U for minimum cost of transport is given by

$$U = \sqrt{V'^2_{\text{hor}} + 2 V'_{\text{hor}} W_{\text{hor}} \cos \alpha + W^2_{\text{hor}}} \quad (90)$$

where α is the horizontal angle of the bird's flight path through the air measured from the direction of the horizontal wind component (Fig. 9). From Figure 8, at constant altitude,

$$V'_{\text{hor}} = \sqrt{V'^2 + W_{\text{vert}}^2} \quad (91)$$

Substituting equations (88) and (91) in equation (90), and rearranging, yields

$$U = f_8(t) \quad (92)$$

and finally, for minimum cost of transport over the ground,

$$\frac{P'_i}{wU} = f_9(t) \quad (93)$$

since P'_i , U and body weight (w) are all functionally related to time. If the equations in this section are evaluated, the minimum cost of transport is found to be virtually constant in time for flight at a constant altitude in a constant wind velocity \bar{W} and at a constant heading α relative to the wind direction. For example, changes in minimum cost of transport over the ground were less than 10% for two simulated birds of different sizes that flew long enough to consume 20% of their initial masses as fuel (fat). The birds had initial masses of 0.0156 kg and 0.156 kg respectively and flew at altitudes of 0 and 6000 m. They encountered winds with horizontal velocity components of 5 m/sec from all directions, and up- and down-drafts of 1 m/sec.

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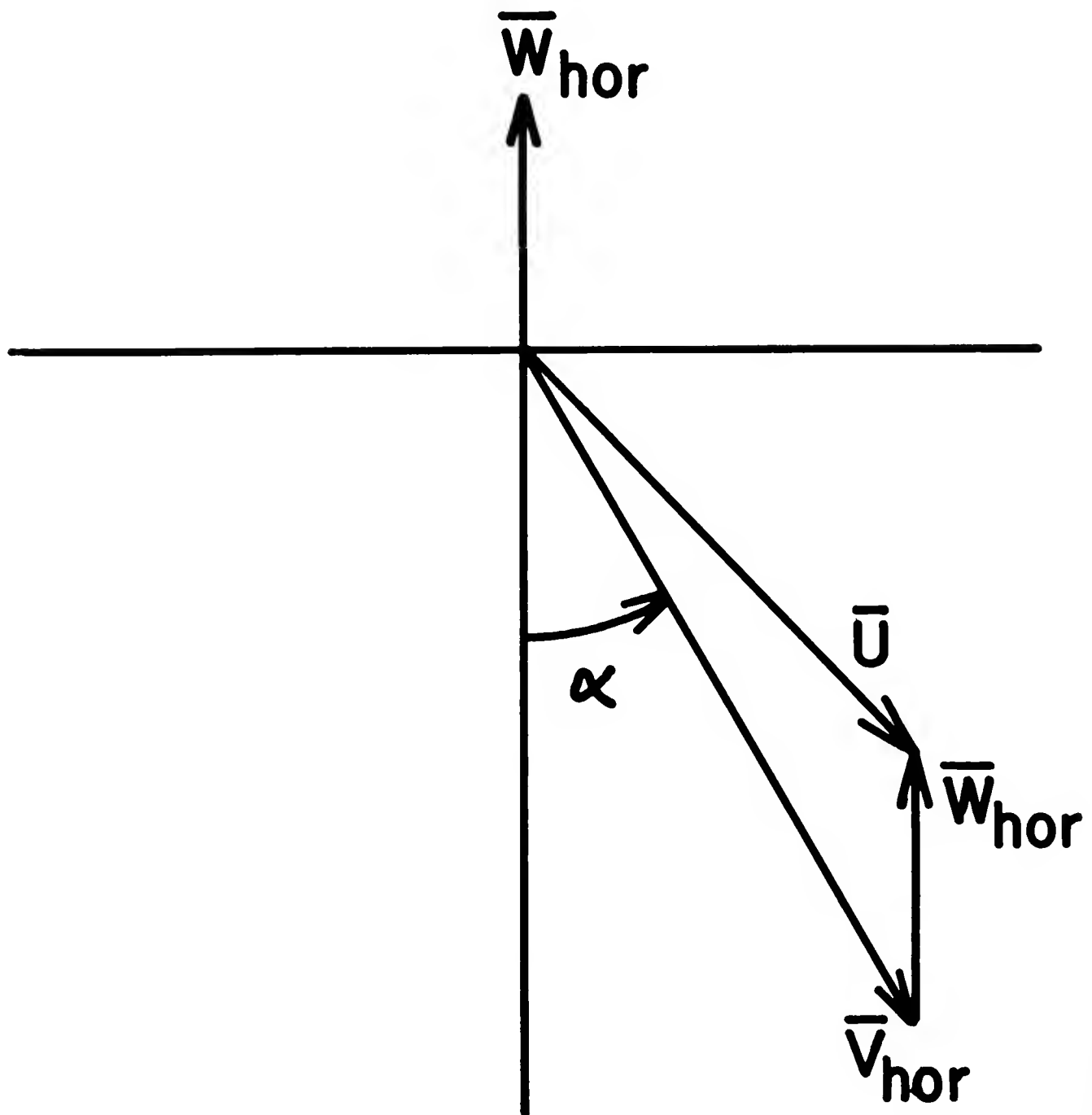


FIG. 9. Ground velocity \bar{U} is the vector sum of the horizontal components of air velocity (\bar{V}_{hor}) and wind velocity (\bar{W}_{hor}).

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DISCUSSION

WILLIAM R. DAWSON: I must be getting old! When I was a graduate student Oliver Pearson calculated that Ruby-throated Hummingbirds would be unable to make it across the Gulf of Mexico, falling into the Gulf short of Yucatán. Now we've escalated the problem to Golden Plovers that may be dropping somewhere between Alaska and Hawaii!

Seriously, however, I hope you can properly appreciate the work, technical ingenuity, and virtuosity that has gone into these analyses. I should now like to ask the discussants to come up and present their comments.

I've asked Dr. Bartholomew to be the first discussant of Tucker's presentation, and I'll turn the microphone over to him.

GEORGE A. BARTHOLOMEW: I think that the presentation that you have just received invites a slightly different treatment from those that I've been directing at previous ones. I'm going to add an addendum which attempts to place what you have just heard into a historical perspective.

The people who have presented this symposium—the four speakers, the three discussants, and the chairman—have an interesting sociological and historical relationship. Kendeigh entered the field of physiological ecology in the late twenties and early thirties and has been active ever since. Odum came in in the early forties, I came in in the late forties, Dawson in the middle fifties, the other speakers have entered the field from the late fifties through the middle to late sixties. Consequently, you have a temporal transect through the study of avian energetics. There has obviously been input from scores and scores of other people, but we here represent a chronological cross-section of the field. It is striking that this particular chronological cross-section has internal coherence. All of us have approached avian energetics by making relatively conventional physiological measurements and then, doing our very best to fit these measurements into an adequate environmental context—for better or for worse, as you can judge from the previous discussion.

Concurrent with the scientific tradition represented by the participants in this symposium, there has been another tradition going on in England which comes in through quite another door. The participants in this other tradition have not thought of themselves as physiological ecologists, but just as physiologists. They have directed their attention in what was essentially a physical and engineering approach to the

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analysis of biological functions. Names such as Hill, Pringle, Gray, Weis-Fogh are familiar to many of you, or most of you, and these people all represent a relatively unified intellectual tradition, just as those of us here represent, loosely defined, a single intellectual tradition.

What has happened with these two traditions is remarkable because they have fused at the only point in which they have actual congruence, and this point is in the analysis of locomotion. In dealing with the problem of moving a body through space and trying to estimate the cost of doing this, the two traditions have approached from opposite directions. Herein lies the importance of what you've just heard; Tucker has been able to fuse these two separate disciplines in a unified interpretation.

I'd like to comment on the work of Colin Pennycuick, because his paper, published in *The Ibis* in 1969, I feel has not received the careful attention it merits from American ornithologists. Most of Pennycuick's publications on the application of helicopter aerodynamic theory to natural flight appear in journals which are not specifically ornithological. Yet his constructs have, for the first time, allowed us to fit what is known of the performance of birds from natural history observations into a substantial theoretical context, which then serves the purpose which Dr. Odum has previously mentioned, of giving us a model which we can use to refine and make more precise the way we look at the world. To me, the beautiful part of the presentation you have just heard is that it brings together the theory derived from one intellectual tradition, and empirical measurements, based on the tradition which most of us here in this room represent. The gratifying thing is that the conclusions from the two different approaches come out essentially the same. And what we find then is the empirical physiological measurement allowing a refinement of the engineering-type theory. What this really says, I think, is that if any of you are studying a bird and you need some estimate of how much it costs to fly on the course which it's flying, to and from nest, gathering food, or migrating, you can do so if you know its wingspan and its weight. From these two parameters, you can calculate how much work this animal is doing as it goes about its activities, because wingspan, wingbeat frequency, and actuator-disc diameter and area, are all related, and the weight tells you how much the animal must actually lift.

Knowing these things, any one of us, however limited his ability to generate the primary formulae, or even to manipulate the secondary formulae, can, by using the tertiary formulae, get values as accurate or more accurate than one could obtain by direct physiological measurement. This represents the kind of fruition we all hope science will yield.

I would like to add one further statement. This entire structure has developed since 1968 when the first of Colin Pennycuick's papers on aerodynamic analysis of flight in pigeons and the first of Vance Tucker's

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papers on flight in budgerigars in air tunnels appeared in the *Journal of Experimental Biology*. Tucker and Pennycuik, by interacting both personally and intellectually, in the brief span of 5 years have brought our understanding of flight to a level of precision that has been achieved in no other aspect of energetics. Lest you think I am being fulsome in my praise, I can assure you that this is partly happenstance, because the phenomenon that was being studied, namely, flight, has more physical constraints than other aspects of avian biology, and for this reason lends itself to precise analysis. In any event we can now take this most characteristic attribute of birds, and feed it back into our natural history studies, our ecological studies, our inquiries about migration and navigation, and in fact all aspects of bird biology, because if one excludes the ratites, and penguins, everything birds do is in one way or another linked to flight.

DR. DAWSON: I'd like now to call on Dr. Kendeigh for a few comments.

S. CHARLES KENDEIGH¹: There is a hint in Dr. Tucker's presentation that heat generated by the muscular activity of flight may be used for body temperature regulation. If true, there would be energy conservation in that the heat generated by flight would compensate for part or all of the supra-basal tissue metabolism required at ambient temperatures below the zone of thermal neutrality. This requires special attention, since other evidence indicates that for both birds (Kontogiannis, 1968; Pohl and West, 1973) and small mammals (Jansky, 1965) the energy expenditure for locomotor activity is additive to that generated for temperature regulation rather than being compensatory. Flight, however, is an especially strenuous activity. The required energy expenditure is so great, and heat production so high, that body temperature in at least some birds is raised and the problem is to get rid of excess heat rather than to conserve it (Hart and Roy, 1967).

If heat production of flight compensates completely for body temperature regulation, then the energy expenditure during flight is independent of temperature. Hart and Berger (1972) show how this may occur. It appears therefore, that in calculating the energy cost of long sustained flights, such as migration, the ambient temperature may be ignored. The energy cost needs to be added to basal metabolism, not to standard or existence metabolism, to obtain the total rate of energy expenditure. The heat increment of feeding introduces an error, if the birds had been feeding previous to taking flight, but this food in small birds is fairly rapidly assimilated and in long flights may be ignored.

¹ For the convenience of the reader, Dr. Kendeigh has elaborated upon his oral presentation and also included references to pertinent literature.—Ed.

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Dr. Tucker is concerned in his presentation with the power functions and energy requirements of sustained flight. Presumably the energy required to take-off from a stationary position and to accelerate to full flight speed would be considerably greater than the energy cost of maintaining flight speed once it is attained. The energy cost of deceleration and alighting on a perch would presumably be less than that of sustained flight. It would be interesting to have quantitative information on these points because small birds in their ordinary daily activities normally fly only very short distances and are continually taking-off and alighting. This is part of their foraging, social, and nesting activities. It is possible that aerial-feeding species, such as the swallows and swifts, although continually flying for long periods of time, spend no more energy in their foraging activities than do species that feed on the ground or in the trees. The energy expenditure in these foraging and other activities involving intermittent and short-term or leisurely periods of flight must certainly be additive to existence metabolism, not compensatory as may hold for the long, strenuous, flights involved in migration. It is important to resolve questions of this sort for the accurate calculation of daily energy budgets.

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DR. TUCKER: Professor Kendeigh has asked a very interesting question that points out one of the limitations of the theory in its present form. The theory describes flight at relatively high airspeeds and accounts for changes in altitude. However, it does not account for acceleration and deceleration. Accordingly it should yield accurate estimates of energy costs for long distance migratory flights in given wind conditions when the mean airspeed for the entire flight is close to the airspeed at the midpoint in time of the flight. But we cannot expect equally accurate estimates for a bird flitting about from bush to bush. In this situation, the mean airspeed is considerably less than that at the midpoint of the flight because of the time span in acceleration and deceleration. The theory could be expanded to include a term for accelerations and might do a pretty good job for predicting the energetic cost of acceleration from one intermediate airspeed to

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another. But the theory does not apply to airspeeds near zero and probably would need substantial modification before it would yield accurate predictions at low airspeeds. Dr. Pennycuick has analyzed the modifications that are required for hovering flight. Furthermore, to evaluate a modified theory for a bird taking off and landing would be a formidable job, since the flight speed, altitude, and wind conditions would all have to be described as functions of time.

My guess would be that a modified theory would give an accurate enough estimate for energy expenditure during take-off to be of use in the energy budgets we've discussed today. But I can't produce anything to substantiate that guess in the way of empirical measurements.

DR. KENDEIGH: Could you give an opinion on the Purple Martin? Does it spend more energy on feeding than a House Sparrow?

DR. TUCKER: The House Sparrow hopping about on the ground?

DR. KENDEIGH: Or making short flights?

DR. TUCKER: It would just be awfully hard. The Purple Martin has a large wingspan for its mass, larger than the average bird of that mass, I would guess. So we can expect its power requirements for flight would be lower than for the average bird, since wingspan is a very important determinant of power requirements for a given speed. I guess the answer depends on how vigorously your House Sparrow hops about.

DR. DAWSON: Thank you for that courageous stance! I would like now to call Dr. Odum to conclude the discussants' remarks, after which I will ask Dr. Tucker if he would entertain some questions from the audience.

EUGENE P. ODUM: Just a couple of things—no more parallels with man and nature this time!

Dr. Tucker has shown in a convenient manner how the engineer's model for airplane flight helps understand and predict bird flight, but there is a difference in components. We've already said that airplanes and birds are approached differently. What Dr. Bartholomew mentioned is very important, I think, and that is the engineer's models are highly parametized, which means that the important components are based on physical constants, quantities one does not have to measure but merely calculates from well established physical laws. The problem with modelling biological systems, of course, is that we don't have the benefit of that kind of precision. We have to rely more on measurements and quantities that have wide variance. But certainly

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for the future, the challenge is to get more parameters in there so the model is less dependent on imprecise measurements.

An illustration of failure in prediction due to poor data relates to hummingbirds. I remember when Pearson, who obtained the first good data on hummingbird metabolism, calculated that a hummingbird couldn't fly across the Gulf of Mexico because the only available measurements of premigratory weight gain indicated only about 1 gram of fat was available for migration. Subsequent to this one of my students, Robert Norris, found that the Ruby-throated Hummingbird puts on $2\frac{1}{2}$ grams of fat just before fall migration, and that just about doubles the body weight temporarily. With this new information flight across the Gulf became easily possible. Thus, I don't think a 50% loss in body weight during migration is at all unreasonable.

APPENDIX

APPENDIX: CONVERSION FACTORS FOR UNITS
USED IN SYMPOSIUM

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(a) TO CONVERT FROM	ABBREVIATION	(b) TO	ABBREVIATION	MULTIPLY BY*
FORCE				
Mass (referred to as "body weight" in some papers) in kilogram**	kg	weight in Newton**	N	9.81 (0.102)
ENERGY				
Cubic centimeter of oxygen (consumed in metabolism)	cm ³ or cc cm ³ O ₂	calorie joule**	cal J	4.8 (0.21) 20.1 (4.98 × 10 ⁻²)
Liter of oxygen (consumed in metabolism)	l l O ₂ l O ₂	kilocalorie kilojoule** joule**	kcal kJ J	4.8 (0.21) 20.1 (4.98 × 10 ⁻²) 20.1 × 10 ³ (4.98 × 10 ⁻⁵)
Calorie	cal	joule**	J	4.187 (0.239)
Kilocalorie	kcal	kilojoule**	kJ	4.187 (0.239)
	kcal	joule**	J	4187 (2.39 × 10 ⁻⁴)
POWER				
Calorie per hour	cal/hr	watt**	W	1.163 × 10 ⁻³ # (859.8)
	cal/hr	milliwatt**	mW	1.163# (0.860)
Kilocalorie per hour	kcal/hr	watt**	W	1.163# (0.860)
Kilocalorie per day	kcal/day	watt**	W	4.85 × 10 ⁻² # (20.62)
LENGTH, DISTANCE				
Foot	ft	meter**	m	0.3048 (3.281)
Mile	mi	kilometer**	km	1.609 (0.621)
SPEED				
Feet per second	ft/sec	meter per second**	m/sec	0.3048 (3.281)
Feet per minute	ft/min	meter per second**	m/sec	5.08 × 10 ⁻³ (196.9)
Kilometer per hour	km/hr	meter per second**	m/sec	0.2778 (3.600)
Miles per hour	mi/hr	meter per second**	m/sec	0.447 (2.237)

* Number in parentheses is the multiplier for converting a quantity with units shown in column (b) to the units indicated in column (a).

** SI units

This multiplier should also be used in converting weight- or surface-specific metabolic rates and thermal conductances (heat transfer coefficients) to SI units (e.g., multiply cal · g⁻¹ · hr⁻¹ by 1.163 × 10⁻³ to obtain W/g, and multiply kcal · m⁻² · hr⁻¹ · °C⁻¹ by 1.163 to obtain W · m⁻² · °C⁻¹)

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